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Mark R. Millikin and Austin B. Williams

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Synopsis of Biological Data on the Blue Crab, *Callinectes sapidus* Rathbun[1]

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ABSTRACT

This synopsis reviews taxonomy, morphology, distribution, life history, commercial hard and soft shell crab fisheries, physiology, diseases, ecology, laboratory culture methodology, and influences of environmental pollutants on the blue crab, *Callinectes sapidus*. Over 300 selected, published reports up to and including 1982 are covered.

INTRODUCTION

The importance of the commercial and recreational fisheries of the blue crab, *Callinectes sapidus* Rathbun, along the Atlantic and Gulf of Mexico coasts of the United States is reflected in the large amount of basic and applied research conducted with this species, both past and present. Life history and the fishery for the blue crab have been described for Delaware (Hall 1976), Chesapeake Bay (Hay 1905; Churchill 1921; Pearson 1948; Van Engel 1958), North Carolina (Pearson 1951), South Carolina (Eldridge and Waltz 1977), Georgia (Palmer 1974), St. Johns River, Fla. (Tagatz 1968a, b), the Atlantic coast states in general (Sholar 1982), gulf coast of Florida (Oesterling 1976), Alabama (Tatum 1979), Mississippi (Perry 1975), Louisiana (Jaworski 1972, 1982; Adkins 1982; Roberts and Thompson 1982), and Texas (More 1969). A partial bibliography by Cronin et al. (1957) and an annotated bibliography by Tagatz and Hall (1971) on the blue crab have served researchers, fishery managers, and commercial crabbers. In view of the continuing contributions to the knowledge of life processes of this species, a synopsis of biological data of *C. sapidus* is presented.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Callinectes sapidus Rathbun 1896.

1.12 Objective synonymy

It is not necessary to cite here all references to descriptions or figures attributable to *C. sapidus*. The synonymy below is a modified version of that given by Williams (1974) and does not distinguish objective and subjective synonyms.

Portunus hastatus Bosc 1802 (eastern North America; not *Cancer* (= *Portunus*) *hastatus* Linnaeus 1767).

Lupa hastata Say 1817 (eastern North America; not *L. hastatus* Desmarest 1823 = *Cancer hastatus* Linnaeus 1767).

Portunus diacantha Latreille 1825 (variety; North America, Antilles, Brazil, etc., types not extant; restricted to Philadelphia, Pa., by Holthuis (1962), and name suppressed by International Commission on Zoological Nomenclature (1964)).

Lupa dicantha Gould 1841 (variant spelling of *P. diacantha* Latreille 1825; also DeKay 1844; Holmes 1858).

Callinectes diacanthus Stimpson 1860 (western Atlantic).

Callinectes hastatus Ordway 1863 (western Atlantic; also A. Milne Edwards 1879; Rathbun 1884; Young 1900).

Neptunus (*Callinectes*) *diacanthus* Ortmann 1894 (Florida; Haiti; Brazil).

Callinectes sapidus Rathbun 1896 (eastern North America and Caribbean).

Callinectes sapidus acutidens Rathbun 1896 (Brazil).

Callinectes africanus A. Milne Edwards and Bouvier 1900 (= a figure of *C. sapidus*).

1.2 Taxonomy

1.21 Affinities

Suprageneric

Phylum Arthropoda
Class Crustacea
Subclass Malacostraca
Order Decapoda
Suborder Pleocyemata
Infraorder Brachyura
Superfamily Portunoidea
Family Portunidae
Subfamily Portuninae

Generic

Callinectes Stimpson, 1860

The generic concept is that of Stimpson (1860), emended by Rathbun (1896), and Williams (1974), who gave the following

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description: Portunid crabs lacking an internal spine on carpus of chelipeds. Abdomen of males broad proximally, narrow distally, roughly T-shaped; first segment broad, almost hidden; second segment broad, slightly overlapping coxae of fifth pereopods at each side; third-fifth segments fused and tapering sinuously from broad third to distally narrow fifth; sixth segment elongate and narrow; telson ovate with acute tip. Abdomen of females exhibiting two forms: Immature females with abdomen triangular from fourth segment to tip of telson, segments fused; mature females with abdomen broadly ovate (excluding telson), segments freely articulated; first segment almost hidden; second and third segments slightly overlapping coxae of fifth pereopods at each side; fifth and sixth segments with greatest sagittal length; sixth segment narrowing distally in irregular broad arc to articulate with triangular telson. Abdomen and telson of both sexes reaching anteriorly beyond suture between thoracic sternites IV and V.

The type-species is *Callinectes sapidus* Rathbun 1896, by designation of the International Commission on Zoological Nomenclature (1964:336).

Stimpson (1860) created the genus *Callinectes* to contain portunids in which the males have a T-shaped abdomen and the merus of the outer maxillipeds is short, sharply prominent, and curved outward at its external angle. Today only Stimpson's abdominal character helps to distinguish *Callinectes* from similar portunid genera, the obvious affinities leading both Stephenson and Campbell (1959) and Stephenson (1962) to challenge the validity of *Callinectes,* although Stephenson et al. (1968) agreed to its distinctness after numerical analysis of 57 characters in 41 species of portunids in 4 genera. Strengthening this position is the lack of an internal distal spine on the carpus of the chelipeds of both the megalopa and all crab stages in *Callinectes,* whereas this spine is always present, occasionally prominent, in all *Portunus* species.

Specific

The following species diagnosis for adult specimens of *Callinectes sapidus* (Fig. 1) is quoted from Williams (1974:779):

"Carapace bearing two broad either obtuse or acuminate, triangular frontal teeth with mesial slopes (incorporating a pair of rudimentary submesial teeth) longer than lateral slopes [Fig. 1]. Metagastric area with posterior width approximately 1.2 times length, anterior width about 2 times length. Anterolateral margins slightly arched; anterolateral teeth exclusive of outer orbital and lateral spine obtuse to acuminate and directed outward more than forward. Much of surface smooth, with scattered granules, but granules concentrated locally on mesobranchial, posterior slope of

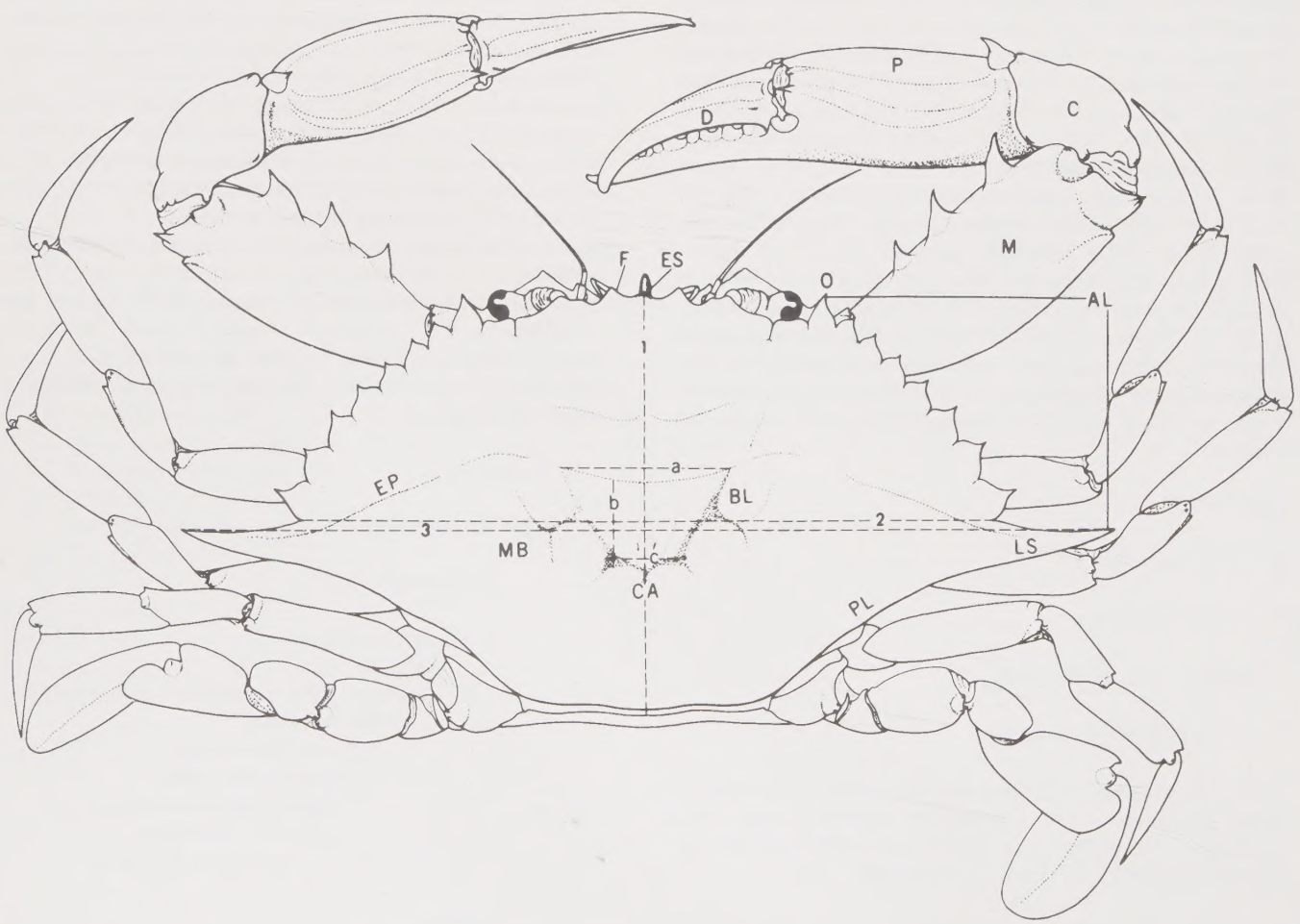


Figure 1.—Mature male *Callinectes sapidus* from North Carolina in dorsal view. Measured features indicated by numbered lines: 1, carapace length; 2, carapace width to base of lateral spines; 3, carapace width including lateral spines; dimensions of metagastric area: a, anterior width, b, length, c, posterior width. Other features include: F, frontal teeth; O, outer orbital tooth; AL, anterolateral teeth; LS, lateral spine; PL, posterolateral margin; EP, epibranchial line; ES, epistomial spine; MB, mesobranchial area; CA, cardiac area; BL, branchial lobe; cheliped: M, merus; C, carpus; P, propodus; D, dactyl (figure reproduced from Williams 1974).

cardiac, and anterior portion of mesogastric area; a tendency to crowding of granules into transverse ridge at summit of cardiac and mesobranchial area in some individuals. Sculpturing of surface varying individually from low to raised relief. Lateral spines varying from rather stout, blunt, and forward trending to slender, elongate, and slightly backward trending. Epibranchial line nearly straight over branchial region, otherwise sinuously curved.

"Propodus and carpus of chelipeds with moderate finely granulate ridges, width of chelae similar, propodal finger of major hand occasionally with lower margin decurved proximally.

"Male abdomen and telson reaching about midlength of thoracic sternite IV; telson lanceolate, much longer than broad; sixth segment of abdomen broadened distally. Mature female abdomen and telson reaching about midlength of thoracic sternite IV; telson with inflated sides almost equilaterally triangular, fifth and sixth abdominal segments equal in length [Fig. 2]. First gonopods of male very long, reaching beyond suture between thoracic sternites IV and V but not exceeding telson; sinuously curved and overlapping proximally, diverging distally, twisting mesioventrally on axis lateral to abdominal locking tubercle and recurving to termination near midline; armed distally with row of large and small retrogressive spinules following ventral and lateral borders with twist of axis; tip membranous, flared portion suggesting an elongate quadrilateral in outline. Gonopores of female paraboloid in outline with apex on long axis directed anteromesad, aperture of each sloping from surface on mesial side under irregularly rounded and linearly wrinkled anterior border superior to bulbous posterolateral border."

Size: A male from Chesapeake Bay measuring 9 in (227 mm) in carapace width has been reported (Williams in press). A female measuring 204 mm across the carapace, including lateral spines, with a length of 75 mm was reported by Williams (1974). He stated (p. 779) that "mature size of females varies considerably, the smallest examined having a carapace length of 21 [mm], width at base of lateral spines 41 [mm], including lateral spines 55 [mm]."

Color: (From Williams 1974:780) "Grayish, bluish, or brownish green of varying shades and tints dorsally on carapace and chelipeds; spines may have reddish tints, tubercles at articulations of legs orange, and legs varyingly blue and white with traces of red or brownish green. Males with propodi of chelae blue on inner and outer surfaces . . . and tipped with red. Mature females with orange fingers on chelae tipped with purple. Underparts off-white with tints of yellow and pink."

According to Williams (1974:780), "Color variations other than those associated with sexual dimorphism and molt cycle are known. Albinos or partial albinos are in museum collections and have been reported both in systematic literature and elsewhere." Other colors reported are: An adult male lacking dorsal green coloration and bright blue and scarlet markings on the legs, the upper surface of the carapace being "robins egg blue" and the appendages paler than usual, but abdomen and underparts with normal color; a bilateral gray and brown colored specimen (summarized by Williams 1974).

Type-specimens: No longer extant.

Type-locality: Restricted to "east coast of United States" (Williams 1965).

For nomenclatural purposes, Holthuis (1962) selected a lectotype from Latreille's (1825) original material from Philadelphia, Pa. It is almost certain that Latreille's material no longer exists, though it is equally probable that his specimens were from North America. By that designation, the "typical" *sapidus* is associated with a population belonging to the eastern United States and particularly to the Middle Atlantic States.

Subspecies: Williams (1974:780) pointed out that "there are morphological variations in this species having far greater systematic interest than size and color." Study of many specimens from throughout the range of the species bears out the conclusion of Chace and Hobbs (1969) that extreme variants "are so different from each other that they could easily be interpreted as distinct species," but there is "no point of demarcation"—morphological, geographic, bathymetric—between the "typical" rather blunt-spined form predominating along the east coast of the United States and the acute-spined form, named *C. sapidus acutidens* by Rathbun, predominating from Florida southward.

According to Williams (1974:780), "Rathbun (1896) characterized the 'acutidens' form (paraphrasing) as being wider than the 'typical' with all prominences more strongly marked, areolations separated by deeper depressions, granules more raised, gastric ridges stronger and more sinuous, a transverse granulate ridge on each cardiac lobe, frontal teeth narrower and more acute and bearing two small intervening teeth, anterolateral teeth broad at base and narrowing abruptly to long acuminate tips with margins granulate,

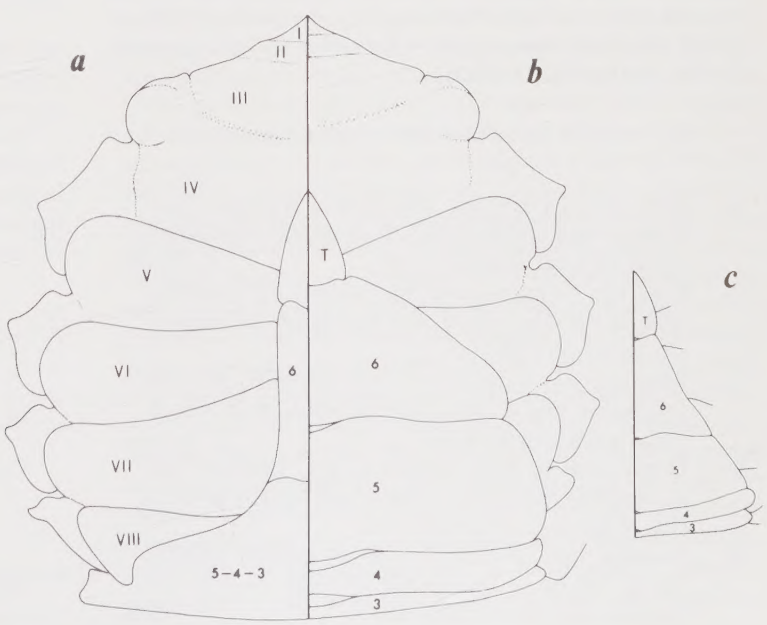


Figure 2.—Composite ventral view of thoracic sternites (Roman numerals), abdomen (Arabic numerals), and telson (T) in situ. a, mature male; b, mature female; c, immature female (figure reproduced from Williams 1974).

lateral spines longer than in 'typical' specimens of equal size, and ridges of chelipeds quite prominent and strongly granulate.

"I thought for a time that a species distributed through approximately 85° of latitude from North Temperate through Tropic to South Temperate Zones might reflect responses to temperature in spination or other characters, 'typical' structure being prevalent in the temperate zones and sharp spination in the tropics, the differences thereby justifying nomenclatural recognition. There is weak but inconsistent evidence for this pattern. Though 'acutidens' individuals are uncommon outside the tropics, intermediates occur everywhere to some degree, and some 'typical' individuals occur in the tropics. Genetic pooling or environmental response reflected in morphology seems poorly structured.

"I consider the whole *C. sapidus* complex to be a single species which has diverged into ill defined populations in certain portions of its range. The 'acutidens' form predominates over most of the latitudinal range, but there are variations. Among these are 'typical' features that reach their most pronounced expression in the population along the east coast of the United States. Taxonomic thinking of biologists has been clouded by the fact that the form originally described was the North American variant which became the standard against which all comparisons were made.

"*Callinectes sapidus* is the member of the genus which has most successfully invaded the Temperate Zone, and in this respect it may be that speciation into forms associated with temperature regimes is progressing, but the process is not yet complete enough that morphological separation is distinct."

A detailed key for identification of the various species of *Callinectes* was presented by Williams (1974). Diagnostic characters of importance for adults include granulation of the carapace, shape and size of frontal and anterolateral teeth, and shape of the male gonopods. Distinguishing characters of various *Callinectes* sp. occurring in the western central Atlantic (lat. 35°N to 5°N; long. 50°W to 95°W) were described by Williams (1978).

Keys to species occurring in eastern and southern United States

Callinectes sapidus is the only species in the genus having 2 broad based, triangular teeth located on the front between the inner orbital teeth. The 7 species of *Callinectes* whose ranges may overlap in parts of the eastern and southern United States can be identified with the aid of the following keys adapted from Williams (1974). Also, color and morphology of these species were discussed by Norse and Fox-Norse (1982).

Key to species based on carapace (excluding juveniles)

1a. Front with 2 prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope ..... *C. sapidus*
1b. Front with 4 teeth between inner orbitals or 2 prominent teeth separated by a space often bearing pair of rudimentary submesial teeth 2
2a. Submesial pair of frontal teeth well developed and more than half as long as lateral pair (measuring from base of lateral notch between teeth) ..... *C. bocourti*
2b. Frontal teeth decidedly unequal in size, submesial pair no more than half as long as lateral pair (measuring from base of lateral notch between teeth) 3
3a. Carapace very smoothly granulated, lines of granules visible but barely perceptible to touch (except epibranchial line variably prominent) ..... *C. similis*
3b. Carapace not so smooth, scattered granules and lines of granules quite evident to sight and touch 4
4a. Carapace coarsely granulated; anterolateral teeth (exclusive of outer orbital and lateral spine) lacking shoulders and swept forward 5
4b. Carapace finely granulated; anterolateral teeth 2-6 (exclusive of outer orbital, 7-8 and lateral spine) with shoulders, not swept forward 6
5a. Anterolateral teeth well separated, all except first 3 and lateral spine with anterior margins concave; chelipeds with ridges finely granulated ..... *C. larvatus*
5b. Anterolateral teeth adjacent, stout, anterior margins not noticeably concave, fifth tooth often largest; chelipeds with ridges coarsely granulated ..... *C. exasperatus*
6a. Submesial pair of frontal teeth absent or vestigial ..... *C. ornatus*
6b. Submesial pair of frontal teeth never vestigial, but no more than half length of lateral pair ..... *C. danae*

Key to mature or nearly mature males based primarily on first pleopods

1a. Tips of first pleopods falling well short of suture between thoracic sternite VI and mesially expanded sternite VII . 2
1b. First pleopods reaching to, almost to, or beyond suture between thoracic sternite VI and mesially expanded sternite VII 4
2a. First pleopods well separated from each other, never touching or crossed; tips not lanceolate 3
2b. First pleopods overlapping each other, often crossed; tips lanceolate ..... *C. ornatus*
3a. First pleopods slender distally, nearly straight, tips bent slightly mesad ..... *C. similis*
3b. First pleopods fairly stout distally, angled toward midline then abruptly bent forward in short slender terminal extension ..... *C. larvatus*
4a. Tips of first pleopods curved abruptly mesad ..... *C. exasperatus*
4b. Tips of first pleopods not curved abruptly mesad 5
5a. First pleopods with tips never extending beyond abdominal locking tubercle on thoracic sternite V, slender distal part almost straight, minutely spined, tips almost always bent ventrolaterally ..... *C. danae*
5b. First pleopods with tips extending beyond abdominal locking tubercle on thoracic sternite V, slender part definitely curved or sinuous, variously spined, never bent ventrolaterally at tip 6
6a. Front with 2 prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope ..... *C. sapidus*
6b. Front with 4 teeth between inner orbitals reaching nearly common level ..... *C. bocourti*

1.22 Taxonomic status

This is a morphospecies exhibiting some variation.

1.23 Subspecies

None. See section 1.21 for discussion on the "forms" of *Callinectes sapidus*.

1.24 Standard common names, vernacular names

Blue crab

1.3 Morphology

1.31 External morphology

Detailed accounts of external morphology of the blue crab are presented by Pyle and Cronin (1950) and in section 1.21 of this synopsis.

1.33 Protein specificity

Polymorphism of several enzymes of the blue crab have been determined. Polymorphic enzymes for both Chesapeake Bay and Chincoteague Bay blue crab populations include: Gonad acid phosphatase, glutamate oxaloacetate transaminase-1, phosphoglucose isomerase, hydroxybutyrate dehydrogenase, malic enzyme, 6-phosphoglucomate dehydrogenase, phosphoglucomutase, esterase, peroxidase, α-glycerophosphate dehydrogenase, and glyceraldehyde-3-phosphate dehydrogenase (Cole and Morgan 1978a). Only the first three enzymes provided reliable zymograms in the gonad, muscle, and green gland tissues, respectively. Monomorphic enzymes for both populations included acid phosphatase of the green gland, adenylate kinase, creatine kinase, esterase (from gonad and gill), hexokinase-1 and -2, lactate dehydrogenase-1 and -2, leucine amino peptidase-1 and -2, malic dehydrogenase, sorbitol dehydrogenase, and xanthine dehydrogenase. Comparison of muscle, eye, and serum protein from adult male crabs from the Choptank River, Md. (8 to 12‰), Backbay, Va. (17 to 20‰), and Chincoteague Bay (35‰) with discontinuous polyacrylamide electrophoresis yielded no differences in muscle protein and low polymorphism in eye and serum proteins (Cole and Morgan 1978b). In adult male crabs, lactate dehydrogenase occurred as one band of activity and 6-phosphogluconate dehydrogenase occurred as two bands of activity following electrophoretic separation from each of seven tissues (muscle, heart, gill, vas deferens, midgut gland, testes, and hypodermis) (Dendinger 1980). Conversely, glucose-6-phosphate dehydrogenase occurred as four bands of activity with different bands in different tissues.

Genetic similarity in the Chincoteague and Chesapeake Bay blue crab populations is suggested from similar percentage polymorphism and similar gene frequencies of the polymorphic enzymes, acid phosphatase, glutamate oxaloacetate transaminase-1, and phosphoglucoisomerase-1. Therefore, Cole and Morgan (1978a) suggested that genetic uniformity is most likely maintained by larval intermixing offshore and that recruitment to estuarine populations of blue crabs is accomplished by immigration of megalopae.

1.34 Aging

Aging of blue crabs is difficult because of the lack of annuli formation on hard body parts. Variation in age to maturity is covered in section 3.12.

1.35 Endoskeleton

A brief description of the endoskeleton was presented by Pyle and Cronin (1950).

1.36 Hemolymph (blood)

Osmoregulation and ionic regulation

Except for the larval stages of development, blue crabs are euryhaline and hyperosmoregulate in the majority of the salinities in which they occur. Blue crabs sometimes occur in freshwater habitats that have access to estuarine waters, at least seasonally (Mangum and Amende 1972). Blue crabs have been reported in freshwater in Louisiana (Gunter 1938), Florida (Odum 1953), Virginia (Mangum and Amende 1972), and Delaware (Ettinger and Blye 1981). Freezing-point depression determinations of blood samples have shown that all adult crabs sampled were hyperosmotic to salinities of 10, 20, and 30‰ (Tan and Van Engel 1966). Males had more ability than females to regulate blood sodium concentrations, especially at a salinity of 10‰, thereby suggesting a physiological adaptation which allows adult male crabs to inhabit low salinities (Tan and Van Engel 1966). Ovigerous females do not regulate as well as nonovigerous, mature females or adult males at salinities of 1.7 or 17‰ (Tagatz 1971). This is consistent with the fact that ovigerous females usually occur in salinities higher than 17‰. Temperatures between 10° and 30°C did not significantly affect the osmoregulatory ability of various stages or sex of blue crabs. According to Leffler (1975a), juvenile blue crabs (30-50 mm carapace width) reared in 25°C, hyperosmoregulate in media of $<$ 700 mOsm/l (25‰ salinity) and conform osmotically at higher salinities. Regarding sodium ions, juvenile blue crabs hyperosmoregulate in environments of up to 720 mOsm/l (26‰ salinity), whereas adult blue crabs hyperosmoregulate below 28‰ (Colvocoresses et al. 1974). Engel (1977) examined the acclimation abilities of the blue crab and *C. similis* to osmoregulate in salinities of 5, 20, and 35‰. In agreement with distribution in natural waters, hemolymph and muscle concentrations of Na^+, Cl^-, and K^+ indicated that adult *C. sapidus* is better adapted for ionic regulation than adult *C. similis* at lower salinities (e.g., 5‰). *Callinectes similis* had significantly lower hemolymph Na^+ and Cl^- concentrations than *C. sapidus* at 5‰. Acclimation at the two higher salinities (20 or 35‰) resulted in similar hemolymph Na^+ and Cl^- concentrations for both species. Engel and Eggert (1974) showed that ovigerous and nonovigerous adult female blue crabs have lower respiration rates than adult male blue crabs at a salinity of 5‰ during summer.

The physiological mechanism allowing blue crabs to hyperosmoregulate was discussed by Mangum and Towle (1977) based upon several experimental studies. Gilles (1973) reported increased $^{14}CO_2$ production as a result of amino acid catabolism, following 120 min exposure of isolated axons of blue crabs to salines consisting of one of two salinities containing one of several uniformly labelled (U-^{14}C) amino acids (arginine, alanine, leucine, glutamate, aspartate, or serine). Oxygen consumption also increased in the diluted medium (850 mOsm/l) compared with seawater (1,100 mOsm/l). Weiland and Mangum (1975) reported that decreased salt concentrations of the blood in blue crabs are accompanied by increases in blood pH. Thereafter, Mangum et al. (1976) demonstrated that male blue crabs (100 to 235 g) produced higher amounts of ammonia (and subsequent higher pH due to combination of $NH_3 + H^+$) when acclimated to salinities of 28 or 5‰ compared with crabs acclimated to 35‰. This is probably the result of increased amino acid catabolism which occurs when blue crabs are located in salinities lower than that of their blood (Gerard and Gilles 1972; Gilles and Gerard 1974). An enzyme believed to be involved in the "salt pump" of the blue crab, $Na^+ + K^+$-dependent ATPase is responsive to increased Na^+ uptake in blue crabs migrating

upstream (Mangum and Towle 1977). Specific activity of this enzyme in gill microsomes from crabs at a salinity of 5‰ was nearly twice the value for crabs acclimated to a salinity of 34‰. Mangum and Towle (1977) suggested that an increase in blood NH_4^+ might increase "extrusion" of Na^+ from the gill cell into the blood. Conversely, Kormanik and Cameron (1981) proposed that ammonia excretion (free base, NH_3) in adult blue crabs occurs via passive diffusion in blue crabs adapted to 28 to 30‰ salinity. These investigators demonstrated that the net excretion rate of ammonia was unchanged by sodium transport inhibitor amiloride or by transfer to Na^+- and K^+-free artificial seawater. Cameron (1979) reported that 33 to 50% of sodium effluxes and 50 to 70% of chloride effluxes from adult blue crabs in freshwater resulted from exchange diffusion, with sodium and chloride transport probably occurring via largely independent, electroneutral processes.

Hemolymph composition

Gleeson and Zubkoff (1977) estimated hemolymph volume (25.4 ± 1.4 ml at 95% confidence intervals) of 9 penultimate instar females weighing 98.2 ± 6.2 g (standard deviation) in the intermolt-white sign molt stages (C_4-D_1).

An ultrastructural study of hemocytes prompted Bodammer (1978) to suggest that granulocytes, hyaline cells, and intermediate cells represent different stages of cytogenesis along a path of cellular differentiation. Granulocytes were broadly oval, less elongate (13.4 to 15.7 μm), and wider (6.8 to 9.3 μm) than intermediate cells. Hyaline cells were slightly round to oval, 7 to 13 μm diameter with centrally located nuclei. Intermediate cells were 13.5 to 19.5 μm long and 6.3 to 9.8 μm wide with eccentric nuclei.

Lynch and Webb (1973a) found that serum protein of intermolt, adult males (20-80 mg/ml) and females (35-100 mg/ml) did not differ significantly. Temperature and salinity did not appear to affect serum protein concentration. Total serum protein increased as ovary weight increased. After egg transfer from the ovaries to the pleopods, a slight decrease in serum protein occurred.

Serum glucose did not differ between males (2.3 to 125.5 mg/100 ml) and females (1.3 to 305.3 mg/100 ml), nor did it vary with reproductive stage of females (Lynch and Webb 1973b). However, molt status of the crabs examined was not monitored. Serum glucose levels were lowest in late summer/early fall in males and "old year class" females. Glucose concentrations rose to yearly high levels during spring and early summer (Lynch and Webb 1973b).

Serum zinc and copper of adult blue crabs have been found to be unrelated to environmental temperature and salinity (Colvocoresses and Lynch 1975). Serum copper (ranging from 35 to 150 ppm) was directly related to total serum protein; probably as a result of copper being a component of hemocyanin. Copper content of blue crab serum ranged from 10.7 to 16.2 mg/100 ml ($N = 6$ at 22‰ salinity) (Mangum and Weiland 1975). Serum zinc (6 to 22 ppm) was also strongly related to total serum protein, possibly as a result of zinc being a cofactor for carbonic anhydrase.

Serum calcium concentrations of females in their penultimate instar were found to be similar regardless of salinity (10, 20, or 30‰) within any one molt stage (Haefner 1964). Late premolt females had 500 to 700 ppm serum calcium, early postmolt females had 250 to 300 ppm serum calcium, and intermolt females had 420 to 450 ppm serum calcium (Haefner 1964).

1.37 Internal anatomy

The digestive, muscular, reproductive, circulatory, respiratory, excretory, and nervous systems, and sense organs of the blue crab were described by Pyle and Cronin (1950). Additionally, Cochran (1935) described the skeletal musculature. Descriptions of ovarian tissue at various stages of sexual maturity include those by Cronin (1942), Hard (1942), and Johnson (1980). A detailed account of the male reproductive system was presented by Cronin (1947). Anatomy and neurophysiology of the fifth pair of pereopods (swimming legs) were described by White and Spirito (1973). Johnson (1980) presented a detailed account of the histology of various blue crab tissues and cell types including connective tissue, cuticle, epidermis, gills, antennal gland and bladder, central nervous system, the gut, circulatory system, hemopoietic tissue and hemocytes, phagocytes, and male and female reproductive systems. Ultrastructural features of the myocardium were described by Hawkins et al. (1977). Special features discussed were components of the myocardial cell, structure of the intercalated discs, and organization of the neuromuscular junctions.

Gill morphometry of the blue crab was described by Aldridge and Cameron (1982). Two types of gill epithelial surface included the site presumed to be for respiratory exchange (0.5 μm in thickness) and the primary site for active ion transport (averaging 10 μm thickness).

An anatomical and cytological description of the mandibular gland of the blue crab was presented by Yudin et al. (1980). The authors believe that this gland has an endocrine function, being actively involved in steroid production.

2 DISTRIBUTION

2.1 Total area

According to Williams (1974), the original range of *C. sapidus* was from Nova Scotia, Maine, and northern Massachusetts to northern Argentina, including Bermuda and the Antilles. However, the species has been introduced into several parts of Europe—Øresund, Denmark; the Netherlands and adjacent North Sea, southwest France; Gulf of Genoa; northern Adriatic; Aegean, western Black, and eastern Mediterranean Sea. Recently, the species has also been reported from Lake Hamana-Ko, central Japan (summarized by Williams 1974, in press).

Williams (1974) recognized 14 species of *Callinectes,* nine distributed in the western Atlantic, three in west Africa (only two of these species are different than those occurring in the western Atlantic), and three in the eastern tropical Pacific. Since that time another species has been described from northern Brazil (Fausto-Filho 1980) and Manning and Holthuis (1981) have revised the African species, disclosing older names as well as separating the amphi-Atlantic species into closely related eastern and western Atlantic species.

Currently, there are 16 recognized species of *Callinectes* as listed under geographic regions below. Almost all records are from shallow coastal waters of continents or islands.

Western Atlantic

Callinectes affinis Fausto-Filho 1980. Cocó River, Fortaleza, Ceará, Brazil (Fausto-Filho 1980).

Callinectes bocourti A. Milne Edwards 1879. New Hanover Co., N.C., Mississippi, and British Honduras through West Indies

and Caribbean Sea to Estado de Santa Catarina, Brazil (Williams 1974; Williams and Williams 1981).

Callinectes danae Smith 1869. Bermuda and New Hanover Co., N.C.; southern Florida and eastern side of Yucatan Peninsula, West Indies, and Caribbean Sea to Estado de Santa Catarina, Brazil (Williams 1974; Perschbacher and Schwartz 1979).

Callinectes exasperatus (Gerstaecker 1856). Bermuda, northeastern Florida, Florida Keys, and eastern Yucatan through West Indies and Caribbean Sea to Estado de Santa Catarina, Brazil, with exception of no records from the Guianas and northern Brazil (Williams 1974, in press).

Callinectes larvatus Ordway 1863. Bermuda and North Carolina, through Florida Keys, West Indies, and continental perimeter of Caribbean Sea to Sao Francisco, Brazil (Williams 1974; Manning and Holthuis 1981).

Callinectes maracaiboensis Taissoun 1969. Lake Maracaibo and to unknown extent in West Indies region, including Jamaica (Williams 1974; Norse 1978).

Callinectes ornatus Ordway 1863. Bermuda and off Cape Charles, Va., through southwestern Florida, northwestern Yucatan, West Indies, and southern Caribbean Sea to Estado de São Paulo, Brazil (Williams 1974, in press).

Callinectes rathbunae Contreras 1930. Gulf of Mexico from mouth of Rio Grande, Texas-Mexico border to southern Veracruz (Williams 1974).

Callinectes sapidus Rathbun 1896. See beginning of section 2.1.

Callinectes similis Williams 1966. Eastern United States and Gulf of Mexico from eastern Long Island Sound, Conn., to off Campeche, Yucatan, Mexico, and Jamaica (Williams 1974, in press).

Eastern Atlantic

Callinectes amnicola (De Rochebrune 1883) (=*C. latimanus* Williams 1974). West Africa from Baie de Saint-Jean, Mauritania, to at least as far south as a lagoon north of Luanda, Angola (Manning and Holthuis 1981).

Callinectes marginatus (A. Milne Edwards 1861). West Africa from Cape Verde Is., and Port Etienne, Mauritania, to central Angola (Williams 1974; Manning and Holthuis 1981).

Callinectes pallidus (De Rochebrune 1883) (=*C. gladiator* Williams 1974). West Africa from Baie de Saint-Jean, Mauritania, to Baia do Lobito, Angola (Williams 1974; Manning and Holthuis 1981).

Eastern Pacific

Callinectes arcuatus Ordway 1863. Los Angeles Harbor, Calif., to southern Peru and Galapagos Islands (Williams 1974).

Callinectes bellicosus (Stimpson 1859). San Diego, Calif., to southern Magdalena Bay; La Paz Harbor around Gulf of California to Topolobampo, Sinaloa, Mexico; apparently absent from extreme southern tip of Baja California (Williams 1974).

Callinectes toxotes Ordway 1863. Cape San Lucas, Baja Calif. (historical record only) to extreme northern Peru; extraterritorial, Juan Fernandez Islands (Williams 1974).

2.2 Differential distribution

2.21 Larvae and juveniles

Early zoeal stages of the blue crab are located in surface waters (Tagatz 1968a; Dudley and Judy 1971; Sandifer 1973; Dittel and Epifanio 1982) of high salinity, usually 20‰ or greater (Perry 1975). Zoeae are planktonic and positively phototropic (Costlow et al. 1959). According to Norse (1977), "the occurrence of [various] *Callinectes* [sp.] in a geographic area [usually] implies settlement from plankton, rather than adult immigration." However, juvenile migrations from high salinity to low salinity areas are important in determining annual recruitment to brackish water areas (Van Engel 1958; Sulkin 1977). Nichols and Keney (1963) sampled *Callinectes* sp. larvae offshore between Cape Hatteras, N.C., and Jupiter Light, Fla. Large numbers of early stage zoeae were collected nearshore with progressively later zoeal stages found 20 to 40 mi (32 to 64 km) offshore. Highest frequency of megalopae occurred beyond 40 mi (64 km) offshore. During a 6-mo sampling period (May to October 1978), first stage blue crab zoeae were most abundant in 5 or 11 m depths in Delaware Bay as opposed to 20 m (Dittel and Epifanio 1982). Sandifer (1973) reported *Callinectes* sp. larvae from daytime samples taken from Chesapeake Bay 1 m below the surface and near bottom from June to November, in salinities ranging from 15.8 to 32.4‰. Most of the larvae (85%) were collected in salinities of 20 to 30‰ just outside the mouth of Chesapeake Bay. Most zoeae occurred in the near surface (1 m depth) samples, whereas megalopae were found only in a few bottom samples (Sandifer 1975). Conversely, Williams (1971) and Smyth (1980) reported that megalopae of *Callinectes* sp. were common in surface samples at night. An extensive monthly quantitative sampling of portunid larvae in Mississippi coastal waters from July 1974 to September 1979 indicated that blue crab megalopae were about equally distributed in surface and bottom waters (Stuck and Perry 1981).

Factors that affect vertical distribution of zoeae and megalopae include light intensity, swimming rate, sinking rate, and barokinetic and geotactic behavior. Also, vertical distribution of blue crab megalopae may be dependent upon base activity levels which may be rhythmic due to exogenous or endogenous control (Sulkin et al. 1979; Sulkin and Van Heukelem 1982). Smyth (1980) suggested that diel increases in abundance of megalopae of *Callinectes* sp. in surface waters at night is a negative phototropic response. Laboratory studies with blue crab megalopae have indicated a low threshold in barokinetic response (0.4 atm), such that megalopae would swim a short distance from the bottom when subjected to artificial pressure increases from above (Naylor and Isaac 1973). These authors speculated that such a barokinetic response would inhibit swimming in surface waters of stratified estuaries where net flow often is seaward, while promoting occurrence in deeper waters which often have a net flow upstream. However, data from previously described sampling studies (Williams 1971; Smyth 1980), suggest that this phenomenon of vertical distribution, with megalopae absent from surface waters, may only occur during daylight. Sulkin et al. (1980) evaluated swimming rate and geotactic and barokinetic responses of blue crab zoeal stages I, IV, and VII. Negative geotaxis (upward movement) occurred in stage I zoeae, a period of transition between negative and positive geotaxis (downward movement) was indicated in stage IV zoeae, and positive geotaxis was indicated in stage VII zoeae. Geotactic behavior may explain why Sandifer (1975) did not obtain any zoeal stages later than stage IV in surface samples (1 m depth) during daylight. Although sinking rate increased 3.2 fold between the first and seventh zoeal stages, swimming rate increased 4.4 fold over the same developmental period; therefore, Sulkin et al. (1980) concluded that sinking rate was not responsible for the geotactic behavior that was measured.

Distribution and recruitment of blue crabs is also affected by temperature-salinity interactions on the megalopal stage. For megalopae maintained at 15°C, average duration of the megalopa stage was found to increase as salinity increased (e.g., 15°C, 20‰ = 34 d before metamorphosis; 15°, 40‰ = 58 d before metamorphosis) (Costlow 1967). Therefore, Costlow and Bookhout (1969) suggested that transport of megalopae to waters below 20°C and high salinities may retard further development to the first crab stage, until megalopae are transported to lower salinities, possibly as an adaptive behavioral mechanism to increase recruitment. Perry (1975) reported the occurrence of *Callinectes* sp. megalopae in salinities as low as 4‰, while most megalopae occurred in salinities > 20‰.

Following larval development, early juvenile stages migrate to lower salinity and shallow waters during summer months; later they move to slightly deeper channels or hibernate during colder months when growth ceases or decreases appreciably in Chesapeake Bay (Van Engel 1958) and Delaware Bay (Cronin 1954). Juvenile blue crab distribution in Mississippi waters was as follows: 1) First and early crab stages (3 to 10 mm) occurred most often in 15 to 20‰, 2) 10 to 20 mm juveniles were most frequently found in salinities < 10‰, and 3) maximum number of crabs (20 to 40 mm) were sampled from salinities below 5‰ (Perry and Stuck 1982). Juvenile and/or adult blue crabs occur in much higher densities in areas covered by eelgrass, *Zostera marina*, than on unvegetated bottoms (Heck and Orth 1980).

2.22 Adults

See section 3.51.

2.4 Hybridization

2.41 Hybrids

None reported.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

Blue crabs are heterosexual and show obvious sexual dimorphism. Immature females have a triangular-shaped abdomen, whereas mature females have a broader, semicircular-shaped abdomen (Fig. 2). Males have a T-shaped abdomen readily distinguishable from either female stage (Fig. 2). Typical coloration differences between adult males and females are described in section 1.21. Histology and external morphology of two bisexual crabs (bilateral gynandromorphs) from separate areas of Chesapeake Bay have been described by Cargo (1980) and Johnson and Otto (1981). Johnson and Otto (1981) indicated that few sperm were in the seminal receptacle of their specimen, indicating that copulation had not been completely successful.

3.12 Maturity

Male blue crabs reach maturity after 18 or 19 postlarval molts, while females reach maturity after 18 to 20 postlarval molts (Van Engel 1958). The abdomen of immature males is tightly sealed to the ventral surface, whereas the abdomen of mature males hangs free or is held in place by a pair of "snap-fastener-like" tubercles (Van Engel 1958). Tagatz (1968a) used the following criteria to identify immature and mature males: Immature males have vasa deferentia that are small and the middle vas deferens is white, while mature males have vasa deferentia with large prominent ducts and the middle vas deferens is bright pink. However, Johnson (1980) observed that the middle vas deferens may be white or only pale pink following copulation, while many large, mature male crabs sampled during winter have a white middle vas deferens. Gray and Newcombe (1938b) approximated the average size at which males attain maturity as 89 mm carapace width, since males attain their highest growth increment per molt at this size. As the terminal molt (maturity molt) in females approaches, dark coloration of the mature, semicircular abdomen shows through the translucent, triangular shaped, immature abdomen within 6 d of the terminal molt (Gleeson 1980). Cronin (1942) and Johnson (1980) described histological changes in female ovarian tissue as maturation approaches, and Hard (1942) described ovarian tissue changes before, during, and after the first and second spawnings.

Time to maturity from hatching is reduced by longer growing seasons varying from 10 to 12 mo in Mississippi (Perry 1975) or Florida (Tagatz 1968a) to 12 to 20 mo in Chesapeake Bay (Van Engel 1958; Lippson 1973). Due to semihibernation in winter, crabs hatched in early summer in Chesapeake Bay reach sexual maturity within 12 to 16 mo, while individuals that are hatched in late summer and early fall reach sexual maturity within 18 to 20 mo (Lippson 1973).

3.13 Mating

Unlike males, which may mate several times, female blue crabs mate only once, while in the soft shell stage (A_1—see section 3.44 for molt stage descriptions) following their terminal molt (maturity or pubertal molt). According to Van Engel (1958), mating may occur day or night and may last for 5 to 12 h. Ablation of the outer flagella of antennules of males in laboratory studies indicated that these portions of the antennules are probably primary chemoreceptors for a female pheromone that triggers male reproductive behavior (Gleeson 1980). The pheromone is believed to occur in the urine of pubertal females. Further work indicated that the aesthetasc tuft on the outer flagellum of the antennule of the male is responsible for detection of pheromones produced by females (Gleeson 1982). Olfactory stimuli are of primary importance in the ability of a red sign pubertal molt female to discriminate sexes prior to mating (Teytaud 1971). Still, a visual stimulus (e.g., a male model) combined with olfactory stimuli (culture water from a mature male) provided more rapid sex recognition. White-sign, pubertal molt females did not respond to the aforementioned stimuli. Also, Teytaud (1971) observed mating activity in mature females in the intermolt stage if they had not mated at the time of their pubertal molt in the laboratory. The female is protected by a male before (Stage D_4), and after (Stages A and B), her terminal molt by being grasped by the male's first pair of walking legs, and held right side up in a "cradle-carry" position under the male (Van Engel 1958; Gleeson 1980; Johnson 1980). The first pair of pleopods of the male are the functional intromittent organs, each receiving spermatophores and semen from the respective penis. The second pair of pleopods are inserted into the posterior foramen of the first pleopods, forcing the spermatophores and semen through the tube-like first pleopods. During copulation, semen and spermatophores are passed from the first pleopods of the male into the paired

oviducts and eventually the seminal receptacles (spermathecae) of the female (Cronin 1947). The majority of mating occurs in low salinity waters since males usually remain in brackish areas during the adult stage.

3.14 Fertilization

Eggs are fertilized when passing from the ovaries to the seminal receptacles before being extruded onto the female's pleopods. Egg extrusion onto endopodites of the female's pleopods may be complete within 2 h (Van Engel 1958).

3.15 Gonads

The male reproductive system consists of paired testes, vasa efferentia, vasa deferentia, external penes, and highly modified first and second abdominal pleopods (Cronin 1947). The anterior vas deferens is the most important storage region for completed spermatophores. Spermatophores that transport sperm are ovoid with an average size of 300 × 225 μm (Cronin 1947). Testes of immature males < 5 cm carapace width contain germinative areas and spermatocytes, but spermatids and mature sperm are not present (Johnson 1980). Males larger than 6.5 cm carapace width have spermatids and mature sperm in some testicular lobes (Johnson 1980). Sperm can survive for at least 1 yr in the female's seminal receptacles (Van Engel 1958).

The female reproductive system consists of the paired ovaries and oviducts, part of which serve as the spermatheca. The most ventral portion of each ovary joins the spermatheca. An opening in the posterodorsal surface of the spermatheca permits the passage of eggs and the oviduct leads to a genital pore on the ventral surface of the sixth thoracic somite (Pyle and Cronin 1950). Hard (1942) used histological techniques to verify stages of ovarian growth and maturation which could be recognized by gross, external appearance. Immediately after copulation the ovary is small and white, whereas the large, pinkish spermathecae are distended with sperm. Following copulation, ova require at least 2 mo to develop, resulting in an increased ovarian size and orange color. Females may ovulate more than once. Before the first ovulation, follicles are expanded. After the first ovulation, the ovary remains large and orange colored and egg shell remnants are on the pleopods after hatching. After the second ovulation, the ovary is collapsed, gray or tan colored, and egg shell remnants again appear on the pleopods after hatching.

3.16 Spawning

Spawning of blue crabs is initiated progressively earlier in the spring at lower latitudes. Typically, blue crabs from Chesapeake Bay spawn in May or June, followed by a second spawning in August (Van Engel 1958). Spawning in North Carolinian waters occurs from mid-March to October (Williams 1971), with peak spawning in Beaufort Inlet, N.C., from June to August (Dudley and Judy 1971). Ovigerous females occurred from March through September in southern South Carolina waters, with peak occurrence in April (Eldridge and Waltz 1977). In St. Johns River, Fla., spawning occurs from February through October, with peak occurrence from March to September (Tagatz 1968a). In Lake Pontchartrain, La., two peak spawning periods for blue crabs are February and March, followed by August and September (Jaworski 1972), with similar spawning periods in Mississippi (Perry 1975). The primary spawning ground along the Gulf coast of Florida is located in Apalachicola Bay (Oesterling 1976).

Sulkin et al. (1976) successfully induced ovarian maturation and spawning in laboratory cultured female crabs following their capture during hibernation in winter in Chesapeake Bay. Ovarian development progressed appreciably more rapidly over a 2.5 mo period at 19°C than at 15°C.

3.17 Eggs

Blue crabs generally produce between 1.75×10^6 and 2×10^6 eggs per spawning (Churchill 1921; Graham and Beaven 1942; Pyle and Cronin 1950; Van Engel 1958). Truitt (1939) reported that egg production during a single spawning ranged from 723,500 to 2,173,300, but total number of females examined and possible reasons for variation of fecundity were not discussed. No published data are available concerning fecundity as a function of female carapace width, length, or body weight. Additionally, no data have been reported on relative amounts of eggs spawned from the first and second spawnings from the same individual in the laboratory. The fertilized eggs extruded from the oviduct are distributed on the setae of the endopodites of all four pairs of pleopods (Pyle and Cronin 1950). Approximate ages of blue crab egg masses (sponges) according to color have been assigned as follows: Yellow to orange = 1 to 7 d since extrusion; brown to black = 8 to 15 d since extrusion (Bland and Amerson 1974). According to Roberts and Leggett (1980), a female blue crab produces approximately 30 g (wet weight) of eggs in a single spawning. Tagatz (1965) recorded egg mass (sponge) weights of females ranging from 24 to 98 g with an average value of 37 g.

Total sterol concentration of eggs does not change appreciably during their development; however, the percent esterified form of sterol decreases appreciably (Whitney 1969). Cholesterol was determined to be the dominant sterol in both free and esterified forms. Palmitic acid and stearic acid were the predominant free fatty acids of blue crab eggs. Steryl esters contained large amounts of palmitic, palmitoleic, and oleic acids. Whitney (1970) concluded that the blue crab requires an exogenous source of squalene and sterols, since they were not synthesized from radioactive labelled acetate-1-^{14}C or mevalonate-2-^{14}C by ovaries or eggs.

Lipid-rich blue crab eggs might serve as a clearance route for toxic, lipophilic compounds. Eggs of blue crabs from selected areas near the James River, Va., had two to three times more Kepone (0.1 to 0.15 μg Kepone per g eggs) than that occurring in backfin muscle (Roberts and Leggett 1980). Nevertheless, further research should examine comparative amounts of Kepone in the hepatopancreas of males and females, before conclusions can be drawn concerning the importance of eggs as a clearance route for toxic, lipophilic compounds. It is unknown to what degree hatchability of eggs or viability of larvae may be affected by this contaminant (Roberts and Leggett 1980).

3.2 Preadult phase

3.21 Embryonic phase

Hatching occurs between 14 and 17 d following spawning (egg extrusion) onto the pleopods at 26°C and between 12 and 15 d at 29°C (Churchill 1921). Hatching occurs in high salinity waters (ca. 23 to 30‰) near river mouths, inlets, and coastal areas. Extruded eggs in the early stages of development are 273 × 263 μm, whereas, just before hatching, eggs are larger (320 × 278 μm)

(Davis 1965). In laboratory studies, successful hatching never occurred at the next lowest experimental salinity (15.6‰) below 20.1‰ (Costlow and Bookhout 1959). All successful hatchlings were first zoeal stage larvae and no prezoeae were observed (Costlow and Bookhout 1959). Similarly, successful hatching occurred in salinities of 18 and 26‰ in a separate study (Davis 1965). Davis (1965) observed blue crab larvae escaping the egg's inner membrane as prezoeae, with subsequent prezoeal ecdysis within 1 to 3 min. Davis (1965) suggested that hatching is promoted by osmotic swelling of the inner membrane which ruptures the chorion, followed by rupture of the inner membrane through mechanical action of the prezoea.

3.22 Larval phase

Development and environmental requirements

Newly hatched blue crab larvae normally develop through seven zoeal stages before transforming to megalopae (Costlow et al. 1959; Costlow and Bookhout 1959), but have successfully metamorphosed to the megalopal stage after only six zoeal stages (Sulkin et al. 1976) or occasionally after an eighth zoeal stage in the laboratory (Costlow and Bookhout 1959; Costlow 1965). Sandoz and Rogers (1944) described prezoeae as lacking a dorsal spine, retaining an embryonic cuticle, having an undeveloped telson, and settling to the bottom without successful metamorphosis. Duration of zoeal development (7 stages) in the laboratory at 25°C and a salinity of 26‰, ranged from 31 to 49 d (Costlow and Bookhout 1959), whereas the average duration of zoeal development that included only six zoeal stages before the megalopa was 35.7 d (Sulkin et al. 1976). Average duration for complete zoeal development (7 stages) ranged from 32 to 43 d in control groups of four separate chemical contaminant studies (Bookhout and Costlow 1975; Bookhout and Monroe 1977; Bookhout et al. 1976, 1980). External morphology of the first and second zoeal stages and third and fourth zoeal stages was described by Hopkins (1943, 1944, respectively). Thereafter, description of all seven zoeal stages plus a supernumerary eighth zoeal stage and the megalopa of hatchery-raised crabs was recorded by Costlow and Bookhout (1959) (see Figs. 3A-10A, 3B-10B). Mortality of zoeal larvae in the laboratory is usually highest during the first two zoeal stages. The optimal salinity and temperature combination for zoeal development was 30‰ and 25°C, respectively (Costlow and Bookhout 1959; Sulkin and Epifanio 1975; Bookhout et al. 1976). Optimal salinity and temperature for the megalopal stage of development of laboratory reared blue crabs was 30‰ and 25°C, with an average duration of 8.4 d and a range of 6 to 12 d (Costlow 1967). Mean total length and selected morphological characteristics for the various larval stages are listed in Table 1.

Costlow (1965) observed a high degree of variability in several zoeal stages of laboratory reared crabs. During zoeal stages I-IV, morphological characteristics were the same as those reported by Costlow and Bookhout (1959). Costlow (1965) found that in later stages some molts were not accompanied by any morphological change, a molt stage was omitted entirely, or a molt resulted in a larva with some characteristics from the previous stage that are usually not retained, as well as some new morphology. Stages V-VI and VI-VII were the most frequent combined stages with abdominal segments and development of pleopod buds more similar to the previous stage and the more advanced characters usually in the anterior portion of the larva.

Laboratory studies demonstrated that if a megalopa lost a cheliped prior to day 4 following the final zoeal molt, then a completely regenerated appendage usually appeared after metamorphosis from megalopa to first crab stage (Costlow 1963a). Chelipeds lost after the fourth day of the megalopal stage were not regenerated until the first or second postlarval molt. Removal of both eyestalks from megalopae within 12 h following the final zoeal molt accelerated metamorphosis to the first crab stage and increased the size of postlarval crabs (Costlow 1963b). Removal of both eyestalks 1 to 5 d following metamorphosis did not affect duration of the megalopal stage. Therefore, molt inhibiting hormone of the X-organ may not be secreted in megalopae more than 1 d old (Costlow 1963b).

A comparative description of larval development of specimens of the blue crab and the lesser blue crab, *Callinectes similis,* from North Carolina waters indicated several minor differences in morphometry between the species which could aid in identification of larval field samples (Bookhout and Costlow 1977). The dorsal spine of *C. similis* was longer than that of *C. sapidus* for each zoeal stage. The rostrum and antennae were usually significantly longer in later zoeal stages of *C. similis* compared with those of *C. sapidus*. Usually, there were more short spines on the telson from zoeal stages IV-VIII in *C. similis*. Also, there were usually more natatory setae on the exopodites of the maxillipeds in stages V to VIII of *C. similis*. The megalopa of *C. similis* had a shorter carapace and longer rostrum and antennae than those of *C. sapidus*. These characters were not useful for identification of *C. sapidus* and *C. similis* from Mississippi waters (Perry and Stuck 1982), possibly due to morphometric variation in different geographical regions.

Laboratory culture

Several proven laboratory methods exist for successful hatching of blue crab eggs. Lochhead and Newcombe (1942) reported 90% hatching success when 8 eggs/cm^2 were reared in white, enamel pans (20 × 26 × 6 cm) in natural water (19 to 21‰ salinity, 24° to 27°C). Sandoz and Rogers (1944) observed prezoeae at hatching in salinities of 10 to 22‰, whereas no prezoeae were observed in crabs hatched in 23.4 to 32‰ salinity. Also, eggs hatched successfully in temperatures from 19° to 29°C. Costlow and Bookhout (1960) cut with fine scissors eggs from previously detached pleopods maintained in seawater of 30‰ salinity and 20° to 30°C, and further dissociated the eggs with glass needles into groups of 100 to 1,000. Groups of eggs were placed in compartmented boxes (9 cm^2) containing 20 ml of freshly filtered seawater treated with penicillin (200,000 units/l). The boxes were then placed on a variable speed shaker (110 to 120 oscillations/min) until hatching. More recently, Bookhout and Costlow (1975) placed setae bearing black eggs (eyes and a visible heartbeat) into plastic compartmented boxes (32.5 × 22.7 cm) in seawater of 30‰ salinity and 25°C, on a variable speed shaker for 60 oscillations/min until they hatched. Sulkin et al. (1980) removed "black eyespot stage" eggs from female blue crabs, culturing sets of approximately 500 eggs in 50 ml of seawater (30‰ salinity, 20°-30°C) which also contained penicillin (60 mg/l) plus streptomycin (50 mg/l) or chloramphenicol (5 mg/l) to improve egg and larval survival. Maximum survival rate for blue crabs reared from newly hatched first stage zoeae to first crab stage in the laboratory has been 40% (Costlow[4]).

[4]J. D. Costlow, Duke University Marine Laboratory, Pivers Island, NC 28516, pers. commun. November 1982.

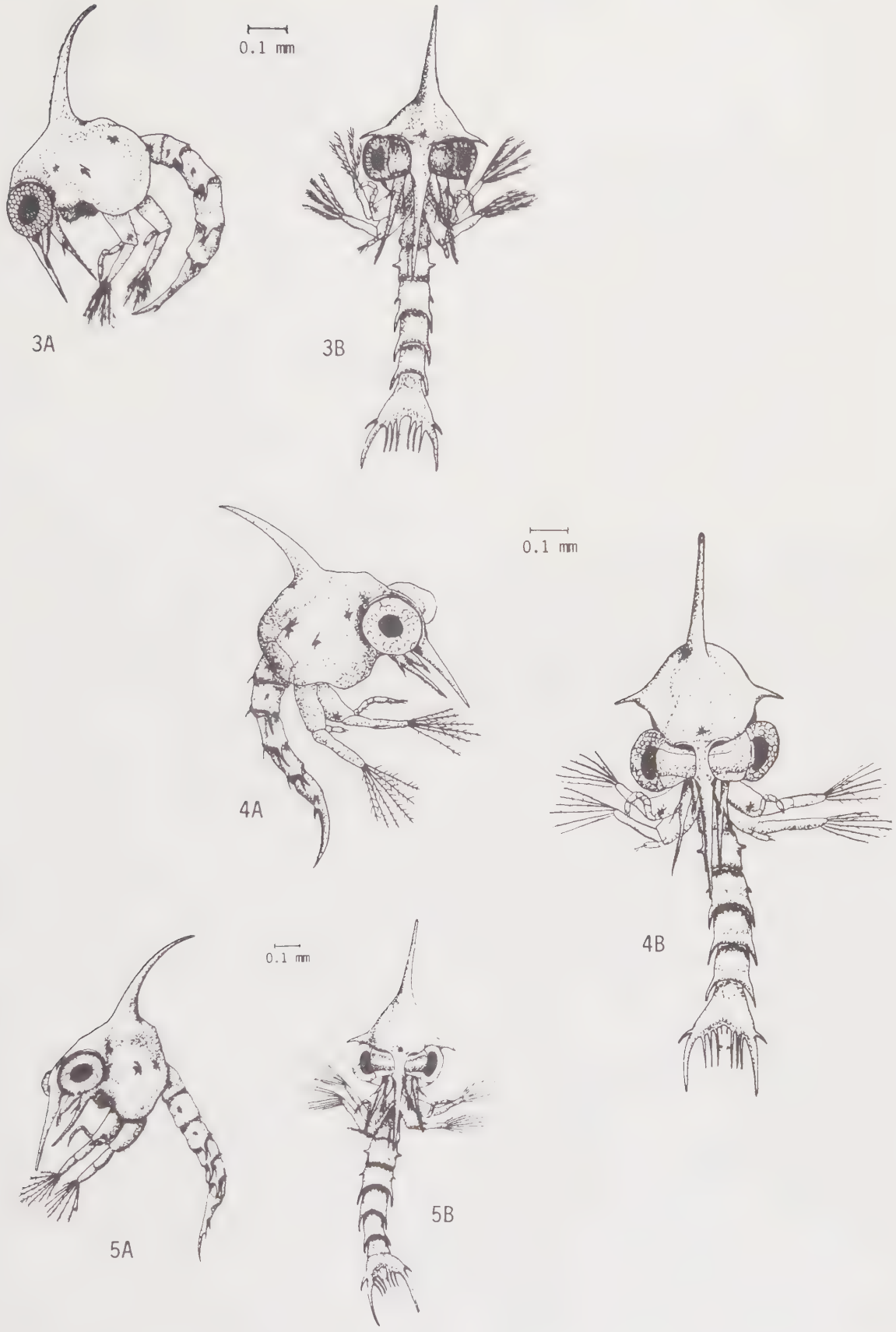


Figure 3.—Side (A) and front (B) views of first zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959). Figure 4.—Side (A) and front (B) views of second zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959). Figure 5.—Side (A) and front (B) views of third zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959).

Table 1.—Selected characteristics of blue crab larval stages of development.

Developmental stage	Mean total length (mm)[1]	Characteristics[2]
Zoea I	1.0	Five abdominal segments plus telson. Eyes are not stalked.
II	1.3	Eyes stalked. Third segment of endopodite of first maxilliped with one additional spine.
III	1.4	Mandible with several small teeth in addition to broad cutting surface. Sixth abdominal segment is present.
IV	1.7	Slight swelling in basal region of antenna indicates beginning of endopodite bud.
V	2.2	Developing endopodite bud larger than in stage IV. Buds of 3rd maxilliped, chela, and pereopods visible beneath carapace.
VI	2.3	Pleopod buds appear on abdominal segments 2 through 6 for first time.
VII	2.8	Terminal aesthetes of antennule increase to 7: 5 subterminal aesthetes added. Basal portion of antennule is swollen.
Megalopa	3.0	Rostrum pointed, longer than antennule, but shorter than antennae. Dactylopod of first pereopod chelate.

[1]From Bookhout and Costlow (1977).
[2]From Costlow and Bookhout (1959).

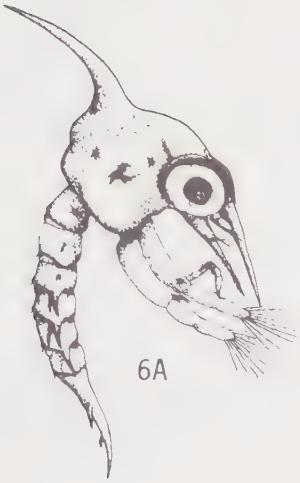
Results of several studies examining the effects of various live food organisms separately or in combination on survival rate and duration of blue crab larval development were reviewed by Millikin (1978). Briefly, it was recommended that the first two blue crab zoeal stages be fed sea urchin, *Arbacea punctulata,* embryos, plus freshly hatched brine shrimp, *Artemia salina,* nauplii, preferably < 12 h old. Since energy content decreases and ash increases over time in starved *Artemia* nauplii (Claus et al. 1979), feeding freshly hatched nauplii to crab zoeae prevents the need to culture *Artemia* nauplii over prolonged periods. Subsequent zoeal stages and the megalopa can be reared entirely on brine shrimp nauplii. Sulkin (1978) recommended feeding rotifers, *Brachionus plicatilis,* to blue crab larvae for the first 14 d of zoeal development, followed by brine shrimp nauplii beginning with the 15th day of development.

Mass culture of blue crab zoeae (approximately 1,000) has been accomplished in large finger bowls (19.4 cm diameter) containing 700 ml of freshly filtered seawater (30‰ and 25°C) which was replaced daily (Bookhout and Costlow 1975). Daily rations consisted of one medicine dropper full of *A. punctulata* embryos for the first two zoeal stages and a similar volume of brine shrimp nauplii for the last five zoeal stages.

Chemical toxicity

Toxicities of the dissolved phase of cadmium and mercury, several chlorinated hydrocarbons, and juvenile hormone mimics or insect growth regulators have been determined for several blue crab larval stages. Megalopae reared at optimal temperature and salinity survived for 1 to 6 d with no successful metamorphosis to the first crab stage when exposed to 250 ppb cadmium in the form of $Cd(NO_3)_2$ (Rosenberg and Costlow 1976). Also, a significant delay in development from the megalopa to third juvenile crab stage and reduced survival rate occurred within each salinity (10, 20, 30, and 40‰) at 50 ppb cadmium compared with 0 ppb cadmium. Blue crab megalopae had similar survival rates when cultured at 25°C in salinities of 20, 30, or 40‰ containing either 5 or 10 ppb mercury ($HgCl_2$) (McKenney and Costlow 1981). Significant reduction in survival occurred in megalopae exposed to 5 or 10 ppb Hg in a salinity of 10‰. Megalopae exposed to 20 ppb Hg experienced significant increases in mortality regardless of salinity (10, 20, 30, or 40‰). Also, average duration of the megalopal stage was significantly longer for individuals exposed to 10 and 20 ppb Hg compared with crabs not exposed to Hg. Methoxychlor (1, 1, 1-trichloro-2, 2-bis (p-methoxyphenyl) ethane) concentrations above 1 ppb (e.g., 1.3 and 1.9 ppb) were acutely toxic to blue crab zoeae, with survival being rare after the third zoeal stage (Bookhout et al. 1976). Average duration from hatching to first crab increased in individuals exposed to 0.7 or 1.0 ppb methoxychlor compared with larvae in the control treatment. Blue crab zoeae exposed to 20 ppb malathion (0, 0-dimethyl phosphorodithionate of diethyl mercaptosuccinate) had reduced survival rate (33%) to the first crab stage and longer average duration (48.6 d) to the first crab stage compared with larvae not exposed to malathion (54% survival and 44.5 d average duration to first crab stage) (Bookhout and Monroe 1977). Acute toxic concentrations (80 ppb or more) caused 10% or less survival of blue crab larvae to the first crab stage and increased duration of zoeal and megalopal development. Mirex (dodecachlorooctahydro-1, 3, 4-metheno-2H-cyclobuta (cd) pentalen-2-one) concentrations of 1 and 10 ppb were acutely toxic to blue crab zoeae, whereas 0.01 and 0.1 ppb mirex were sublethal concentrations (Bookhout and Costlow 1975). Kepone (decachlorooctahydro-1, 3, 4-metheno-2H-cyclobuta (cd) pentalen-2-one) concentrations of 0.5 and 0.75 ppb were sublethal to blue crab zoeae (increased duration between hatching and metamorphosis), whereas 1.0 ppb caused a reduced survival rate of 5% to the first crab stage compared with 22% in the control group (Bookhout et al. 1980). A juvenile hormone mimic, MONO-585 (2,6-di-t-butyl-4-(α,αdi-methyl benzyl) phenol) was acutely toxic (100% mortality) to blue crab megalopae exposed to 10 ppm (Costlow and Bookhout 1979). Also, concentrations of 1 ppm MONO-585 reduced survival to the first crab stage from 100 to 40% at a constant temperature of 25°C combined with a salinity of 20 or 35‰. Culturing megalopae in 5°C, 24 h cyclic temperature regimes (20° to 25°C, 25° to 30°C, or 30° to 35°C) did not result in any significant change in survival of the control group or megalopae exposed to 0.1 ppm MONO-585, whereas some reduction in survival occurred in megalopae exposed to 1.0 ppm MONO-585 in each cyclic temperature regime. Another juvenile hormone mimic, methoprene (isopropyl 11-methoxy-3, 7, 11-trimethyl-dodeca-2, 4-dienoate), showed no toxicity to megalopae exposed to 0.1 or 0.01 ppm in salinities of 15, 25, and 35‰ combined with either 25° to 30°C or 30° to 35°C, 24 h cyclic temperatures (Costlow and Bookhout 1979). Survival was reduced slightly for megalopae exposed to 0.1 ppm methoprene at a cyclic temperature of 20° to 25°C at all salinities. Costlow (1979) evaluated the effects of Dimilin (diflubenzuron), an insect growth regulator, on average duration of the megalopal stage of blue crabs and survival rates of megalopae to the first crab stage. Concentrations of 0, 0.1, 0.3, 0.5, 1.0, 3.0, and 6.0 ppb were combined with one of six different temperature (20°, 25°, or 30°C) and salinity (20 or 30‰) combinations. Percentage survival for megalopae reared in 0.5 or 1.0 ppb Dimilin combined with 20°C plus 20 or 30‰ was similar to that in the control series. However, 3 or 6 ppb Dimilin combined with 20°C plus 20 or 30‰ caused 95 or 100% mortality of megalopae. All salinities

Figure 6.—Side (A) and front (B) views of fourth zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959). Figure 7.—Side (A) and front (B) views of fifth zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959). Figure 8.—Side (A) and front (B) views of sixth zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959).



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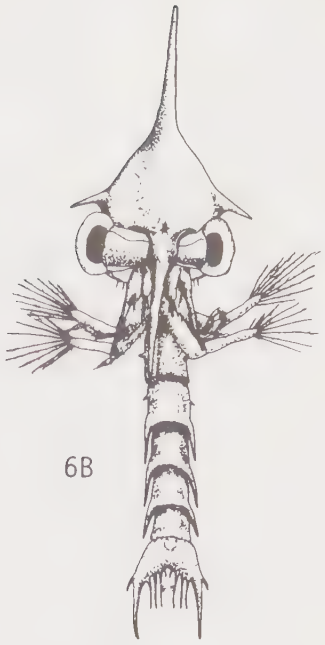

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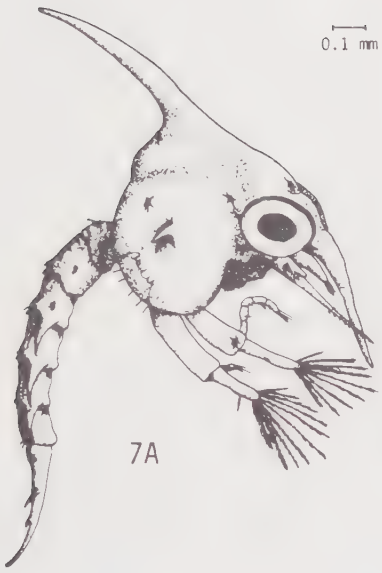

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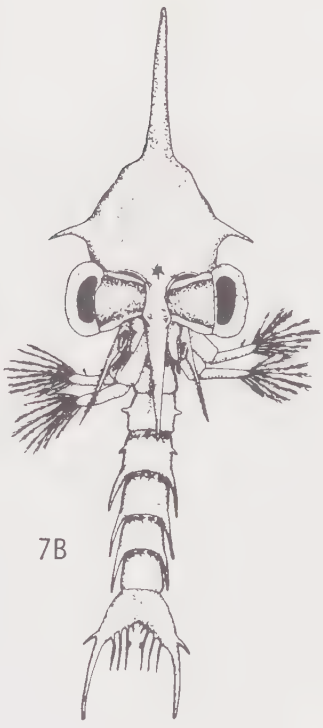

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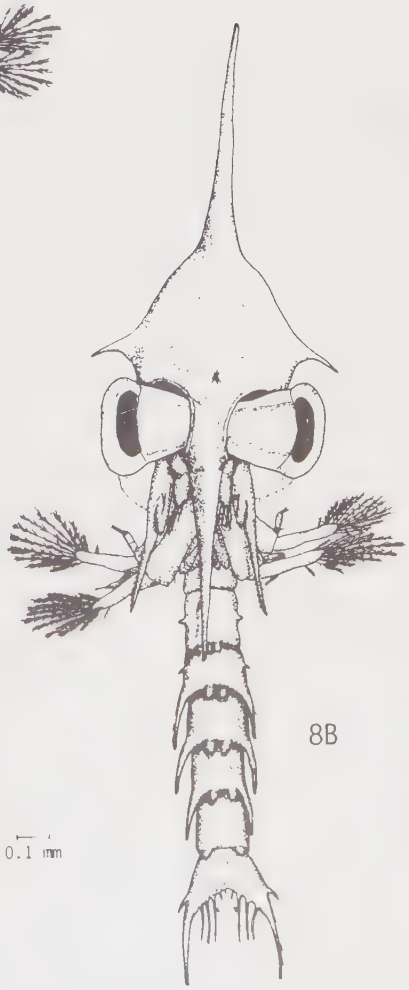

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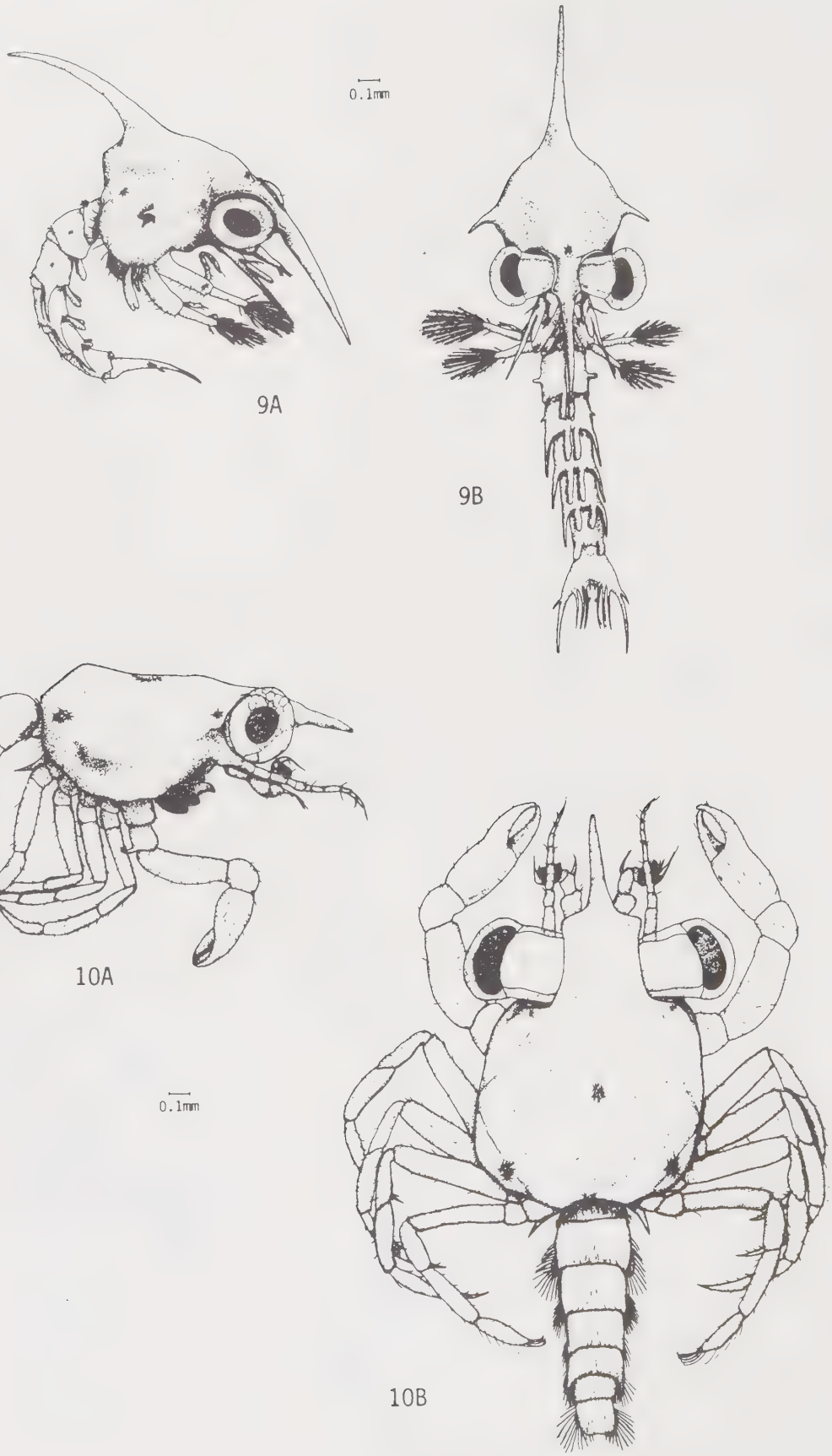

Figure 9.—Side (A) and front (B) views of seventh zoeal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959). Figure 10.—Side (A) and front (B) views of megalopal stage of *Callinectes sapidus* (from Costlow and Bookhout 1959).

combined with 30°C resulted in 100% mortality at 0.5 to 1.0 ppb Dimilin. Average duration of the megalopal stage decreased as temperature increased from 20° to 30°C in the control group or concentrations of 0.1 and 0.3 ppb Dimilin.

3.23 Juvenile phase

Temperature acclimation

Thermal tolerance limits of blue crabs are dependent on acclimation temperature and salinity. Tagatz (1969) evaluated maximum and minimum median thermal tolerance limits (48 h) of juvenile blue crabs (40 to 60 mm carapace width) and adult blue crabs from St. Johns River, Fla., acclimated in 35 or 7‰ salinities combined with 6°, 14°, 22°, or 30°C. Adult females and both sexes in the juvenile stage were less tolerant than adult males to temperature extremes at 7‰ salinity. At both low and high salinities, the upper and lower tolerance limits increased as acclimation temperature increased. The upper thermal tolerance limit was about 37°C for juveniles and adults, while the lower median thermal limit was 3°C when crabs were acclimated to 7‰ salinity and 30°C. Adult blue crabs from South Carolina were found to have an upper thermal tolerance limit of 35.2°C in 36‰ and a lower thermal tolerance limit of 3.2°C in 8.6‰ over 96 h (McKenzie 1970). Blue crabs were less tolerant to low salinities at high temperatures and high salinities at low temperatures.

Laboratory culture

Culture of juvenile stage blue crabs has been highly successful when crabs resulted from individuals hatched in the laboratory and juveniles were assigned separate compartments to prevent cannibalism. Blue crabs, starting with the first juvenile crab stage, attained 94% survival (375 of 400) to a size of 25 mm carapace width (1.25 g) and 88% survival from the first crab stage to 40 mm carapace width (6.0 g) in the laboratory (Millikin unpubl. data). For crabs beginning with the first juvenile stage, culture conditions included individual rearing in plastic urine cups (100 ml) containing artificial seawater of 25‰ salinity at 23°C, an 8-h light, 16-h dark photoperiod, ad libitum feeding three times daily over an 8-h period with live, adult brine shrimp from San Francisco or San Diego, but not Utah (see Bookhout and Costlow 1970), and daily replacement of 100% of the culture water (Millikin unpubl. data). Culture conditions for juvenile blue crabs between 40 and 70 mm carapace width were similar to methods for smaller juveniles except for reduced salinity (20‰ or less) and larger rearing containers (Millikin et al. 1980).

Juvenile blue crabs (initial carapace width ranging from 5 to 40 mm) sampled from Galveston Bay showed maximum weight gain at 29° to 30°C in the laboratory over a 45-d period (Holland et al. 1971). Temperatures above 30°C (up to 35°C) reduced growth of juvenile crabs in the same study. Salinity values < 1‰ caused high mortality rates of juvenile blue crabs (5 to 40 mm carapace width), at a temperature of 29°C, but not at 15°C (Holland et al. 1971).

Design and construction of closed recirculating seawater systems for juvenile blue crabs during intermolt are described by Ogle et al. (1982). These researchers recommended that research be conducted concerning excretion rates, nutrient requirements, and respiration rates of crabs to improve design of closed systems for rearing juveniles and adults.

Chemical toxicity

Several pesticides and other chemicals have been tested for toxicity to juvenile stages of the blue crab. Lowe (1965) reported in a preliminary study that individuals averaging 27 mm carapace width died within a few days of exposure to DDT (1, 1, 1-trichloro-2, 2-bis (p-chlorophenyl) ethane) concentrations > 0.5 μg/l, while exhibiting extreme irritability, increased sensitivity to external stimuli, and finally, paralysis. Mirex was determined to be a more potent stomach poison than DDT for juvenile crabs (35-50 mm carapace width), since lower internal concentrations of mirex (0.02 to 0.2 ppm) than DDT (0.8 ppm) were required to increase metabolic rate (Leffler 1975b). Internal concentrations of 0.02 ppm mirex were accompanied by inhibition of the autotomy reflex. Also, juvenile crabs were slightly more sensitive to mirex when reared in dilute (50 mOsm/l) or concentrated (1,000 mOsm/l) media compared with individuals reared in 200 or 600 mOsm/l. No acute effects were elicited by four weekly feedings of 0.53 μg DDT over a 35-d period, whereas three weekly feedings of 0.14 μg mirex over a 35-d period produced acute poisoning in juveniles (ca. 35 to 45 mm carapace width). In a separate study, mirex leached from fire ant, *Solenopsis richteri,* bait caused significant mortality of juvenile blue crabs (21 to 75 mm carapace width) over a 28-d period at average concentrations of 0.06 μg/l (fall) or 0.12 μg/l (summer) (Tagatz et al. 1975). Growth (percent increase of carapace width) was not affected by concentrations ranging from 0.04 to 0.12 μg/l of mirex over a 28-d period. Juvenile blue crabs (mean carapace width = 34 mm) were shown to have a 96 h LC_{50} to Kepone of > 210 μg/l (nominal concentration), since this was the highest of a set of experimental concentrations, none of which were toxic (Schimmel and Wilson 1977). Juvenile blue crabs (mean carapace width = 37 mm) fed 0.5 g eastern oyster, *Crassostrea virginica,* muscle contaminated with 0.25 μg Kepone/g tissue twice weekly, for 4 wk, accumulated 0.1 μg Kepone/g in muscle (Schimmel et al. 1979). No Kepone was detected in muscle or whole body tissue of blue crabs exposed to 0.3 μg/l Kepone for 28 d. Juvenile blue crabs (mean carapace width = 28 mm) fed 0.5 g of oyster muscle contaminated with 1.9 μg Kepone/g tissue twice weekly for 8 wk had an 80% mortality rate. Gross external signs of Kepone poisoning were characterized as excitation, followed by several days of lethargy, then death (Schimmel et al. 1979). Cadmium and chromium toxicity in terms of LC_{50}'s at 24, 48, 72, and 96 h to juvenile blue crabs (mean carapace width = 1.5 cm) decreased appreciably with increasing salinity (1, 15, or 35‰ salinity) as shown in Table 2 (Frank and Robertson 1979). Juvenile blue crabs (mean carapace width = 2.6 mm) evaluated for toxicity to bromine chloride had a 48-h LC_{50} (median concentration) of 1.2 mg/l and a 96-h LC_{50} (median concentration) of 0.8 mg/l (Burton and Margrey 1978). Median time to death for the same size crabs at 1.6 mg bromine chloride/l was 36 h. Fluoride concentrations of 20 mg/l decreased growth increment per molt of juvenile crabs (mean carapace width = 70 mm) by 4.5% (Moore 1971). Juvenile blue crabs weighing between 25 and 40 g assimilated portions of radiolabelled paraffinic and aromatic hydrocarbons such as benzo(a)pyrene and naphthalene, chiefly in the hepatopancreas, which contained metabolites in the form of dihydroxy compounds and their conjugates (Lee et al. 1976). Highly polar metabolites were found in the green gland, probably in readiness for excretion. Juvenile blue crabs (1 to 8 cm carapace width) exposed to 1 ppm benzene had significantly longer intermolt periods (50 vs. 33 d) and slower rates of limb regenera-

Table 2.—Cadmium and chromium toxicity to juvenile blue crabs in several salinities.[1]

Time (h)	Salinity	LC_{50} (cadmium, mg/l)	LC_{50} (chromium, mg/l)
24	1	1.25	48
	15	13.8	142
	35	34.1	171
48	1	0.9	39
	15	9.4	126
	35	23.8	130
72	1	0.65	36
	15	7.4	98
	35	17.8	114
96	1	0.32	34
	15	4.7	89
	35	11.6	98

[1]From Frank and Robertson (1979).

tion following induced autotomy compared with individuals not exposed to benzene (Cantelmo et al. 1981).

3.3 Adult phase

Laboratory culture

Adult blue crabs are easily cultured in the laboratory in either freshly filtered seawater or artificial seawater, if crabs are reared individually to prevent cannibalism. Maximum and minimum median thermal tolerance limits (48 h) of adult crabs were reported by Tagatz (1969) (see section 3.23). Designs for closed recirculating culture systems include those for peeler crabs (Perry et al. 1982) and intermolt crabs (Biddle et al. 1978; Ogle et al. 1982). Descriptions of shedding tanks in natural waters and closed systems include those by Haefner and Garten (1974) and Perry et al. (1982), respectively (see section 7.5).

Chemical toxicity

Several pesticides and toxic inorganic contaminants have been evaluated with respect to their effects on adult blue crabs. Adult blue crabs (120 to 167 mm carapace width) that were exposed to either 0.01, 0.1, or 1.0 ppm DDT (dissolved) for 12 h, showed a pattern of gill absorption, hemolymph transport, and biotransformation of DDT to DDD (1, 1-dichloro-2, 2-bis (p-chlorophenyl) ethane) and DDE in the hepatopancreas over a 240-h period (Sheridan 1975). Exposure to either 0.1 or 1.0 ppm of DDT for 12 h, resulted in hepatopancreatic accumulation levels of DDT ranging from 100 to 800 ppb (wet weight) over 12 to 240 h following exposure, 70 to 300 ppb of DDD, and 60 to 280 ppb of DDE over the same time period. High mortality rates of blue crabs in salt marshes off Alligator Harbor, Fla., in November and December 1973, were attributed to reduced temperatures (below 18°C) and high body burdens of DDT (Koenig et al. 1976). Crabs from salt marshes that were highly contaminated from DDT and its metabolites had hepatopancreatic concentrations ranging from approximately 1.4 to 39 ppm total DDT (DDT plus its metabolites). Schoor (1974) suggested that dissolved mirex is absorbed through the gills of adult blue crabs because hemolymph had traces of mirex-^{14}C after 5 min of exposure and the hepatopancreas had labelled mirex after 15 min. Mean Kepone concentration of backfin muscle in ovigerous blue crabs sampled from the lower James River, Va., was < 0.05 μg/g (Roberts and Leggett 1980). Eggs had approximately three times more Kepone than in muscle connected to the fifth pair of pereopods. Further study indicated that adult male crabs had higher Kepone concentrations in backfin muscle than females (Roberts 1981). Higher Kepone concentrations usually occurred in the ovary (≥ 0.2 μg/g) compared with backfin muscle (< 0.1 μg/g) of ovigerous and nonovigerous females from the lower James River. Nonovigerous females generally concentrated more Kepone into the ovary than ovigerous females. Two cadmium-binding proteins (molecular weight = 10,600 and 9,400) were isolated from the hepatopancreas of adult blue crabs following successive laboratory injections of cadmium chloride over 3 d of 10, 50, and 100 μg cadmium/d (Wiedow et al. 1982). Adult blue crabs exposed to either 1×10^{-6} M, 5×10^{-5} M, or 5×10^{-3} M of pentachlorophenol or 2,4-dinitrophenol had reduced respiration rates at the highest concentration of either pesticide (Cantelmo and Ranga Rao 1978). Several enzyme activities of mature blue crabs were measured following injection with either sodium pentaclorophenol (Na-PCP) or dinitrophenol (DNP) at a rate of 6 μg/g body weight, or the hepatopancreas was removed and subjected to Na-PCP or DNP in in vitro experiments (Rao et al. 1979). Fumarase, malate dehydrogenase, succinate dehydrogenase, pyruvate kinase, and lactic dehydrogenase were inhibited by Na-PCP and DNP under both in vivo and in vitro conditions. Microsomal Ca^{++}-ATPase from blue crab hepatopancreas was also inhibited by Na-PCP and DNP under in vivo and in vitro conditions.

3.31 Longevity

Tagatz (1968a) reported that few blue crabs survive more than 1 yr after reaching maturity (2 yr of age) and estimated a maximum age of 4 yr for individuals from the St. Johns River, Fla. Van Engel (1958) estimated maximum age of blue crabs in Chesapeake Bay to be 2 to 3 yr.

3.32 Hardiness

Oxygen

Abnormally high local mortalities of blue crabs in commercial pots have been observed in Chesapeake Bay (Carpenter and Cargo 1957) and Mobile Bay (Tatum 1979), probably due to low dissolved oxygen concentrations. Several experiments by Carpenter and Cargo (1957) evaluated the effects of low dissolved oxygen concentrations on blue crabs off the western shore of Chesapeake Bay, slightly north of the mouth of the Patuxent River. No mortality was observed in 34 blue crabs exposed for 24 h to 1.8 mg/l of dissolved oxygen at 30 m, while 70% mortality occurred when 32 crabs were exposed to 0 mg/l of dissolved oxygen for 13 h. The authors concluded from these and several other studies, that at 28° to 30°C, 25% or greater mortality occurred with oxygen concentrations of 0.6 mg/l or less over 24 h and at 24° to 26°C, significant mortality occurred at oxygen concentrations of 0.5 mg/l or less over 24 h.

3.33 Competitors

Occurrence of other species of *Callinectes* in the same areas as *C. sapidus* implies competition among them for food. In the St. Johns River, Fla., *Callinectes similis* and *C. ornatus* occurred up to 13.5 km (25 mi) upstream along with *C. sapidus* in the main river (as low as 15‰ salinity) and in some tributaries (as low as 1‰

salinity) (Tagatz 1967). A general description of total distribution of the various *Callinectes* species is in section 2.1.

Several other crab species such as the mud crab, *Panopeus herbstii,* the stone crab, *Menippe mercenaria,* and the shore crab, *Carcinus maenas,* cohabit with the blue crab in certain geographical regions and prey on similar organisms (Williams and Duke 1979).

3.34 Predators

Predators of blue crabs include numerous fish species as well as other blue crabs. Blue crabs are especially subject to predation during molting and following molting while still in the soft shell stage. Lack of sufficient cover, such as eelgrass, to provide refuge may have an appreciable effect on rate of predation upon the blue crab. Jaworski (1972) reported that black drum, *Pogonias cromis,* red drum, *Sciaenops ocellata,* and the American eel, *Anguilla rostrata,* are important predators of blue crabs in the Lake Pontchartrain estuary of Louisiana. Forty-one percent of stomachs examined from young (60-110 cm total length) sandbar sharks, *Carcharhinus plumbeus,* from Chincoteague Bay, Va., contained blue crabs (Medved and Marshall 1981). Blue crabs occurred in 11.1% of 131 small (95 to 198 mm SL (standard length)) Atlantic croakers, *Micropogonias undulatus,* and 4.6% of 119 large (200 to 350 mm SL) Atlantic croakers from Mississippi Sound (Overstreet and Heard 1978b). Blue crabs first appeared in stomach contents of red drum at 40-49 mm SL, assuming importance in the diet of red drum of 70-79 mm SL (Bass and Avault 1975). Blue crabs were the predominant species of crustaceans (42% occurrence) in red drum of 250-932 mm SL (Boothby and Avault 1971). Blue crabs occurred in 31% of the digestive tracts of 16 red drum (43 to 102 cm SL) from Sapelo Island, Ga., and 17% of 104 red drum (190 to 780 mm SL) examined from Mississippi Sound (Overstreet and Heard 1978a). Soft blue crabs are a major prey item of the American eel (Wenner and Musick 1975). The blue crab was a major food item of the American eel (300 to 700 mm SL) sampled in the James River, Va. (33.3% of total food volume), York River, Va. (68.2% of total food volume), and the Rappahannock River, Va. (35% of the total food volume). Oyster toadfish, *Opsanus tau,* American eel, and white catfish, *Ictalurus catus,* were the three major predators of softshell blue crabs captured in habitat pots and peeler pots in the Wando River estuary, S.C. (Bishop[5]). Spotted gar, *Lepisosteus oculatus,* prey heavily upon blue crabs along the Mississippi Gulf Coast, especially in salinities of 2 to 10‰ (Goodyear 1967). Adult striped bass, *Morone saxatilis,* prey heavily upon blue crabs during May in Albemarle Sound, N.C. (42.2% occurrence) (Manooch 1973). Several freshwater fishes including alligator gar, *Lepisosteus spatula,* spotted gar, and largemouth bass, *Micropterus salmoides* (Lambou 1961), in waters adjacent to brackish water feed upon blue crabs.

Herring or menhaden species which consume zooplankton during some life stages are probably important predators of blue crab larvae. Van Engel (1958) speculated that chief predators of blue crab larvae might include jellyfishes, comb jellies, and fish larvae.

3.35 Diseases, parasites, and commensals

Diseases

Viral infections

Eight viruses have been found in the blue crab (Table 3). Several are pathogenic singly or in combination. Reolike virus (RLV), singly or in combination with Rhabdolike virus-A (RhVA), causes fatal infections characterized by weakness, decreased clotting ability of the hemolymph, and eventual paralysis (Johnson 1977d, 1978). Herpeslike virus (HLV) also causes fatal disease. The crab becomes progressively weaker, with no external or internal signs until shortly before death, when the hemolymph becomes a chalky white (Johnson 1977b, c). Laboratory-reared juvenile blue crabs with HLV had several external signs shortly before death (usually 24 h or less) including: 1) Darkened and/or retracted eyestalks, 2) extension of chelae, 3) anorexia, and 4) loss of equilibrium (anterior facing down) (Biddle et al. 1978). Hemolymph was often chalky white with lack of normal clotting and the hepatopancreas

[5]J. M. Bishop, South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412, pers. commun. October 1982.

Table 3.—Viruses of blue crabs.

Name	Probable taxonomic affinities	Size (nm) (including envelope if present)	Shape	Enveloped	Location in cell	Main tissues and cells attacked	References
RLV (Reolike virus)	Reoviridae	55-60	Icosahedral	No	Cytoplasm	Many types, esp. hemocytes, hemopoietic tissue, glia, epidermis	Johnson and Bodammer (1975) Johnson (1977b,d)
CBV (Chesapeake Bay virus)	Picornaviridae	30	Icosahedral	No	Cytoplasm	Ectodermally derived, esp. nervous tissues; also hemocytes	Johnson (1978)
RhVA (Rhabdolike virus-A)	Rhabdoviridae	20-30 × 110-170 and 20-30 × 600	Bacilliform and elongate	Yes	Cytoplasm	Many meso- and ectodermally derived tissues	Jahromi (1977) Yudin and Clark (1978, 1979)
RhVB (Rhabdolike virus-B)	Rhabdoviridae	50-70 × 100-170	Bacilliform	Yes	Cytoplasm	Mandibular organ	Yudin and Clark (1978)
EHV (Enveloped helical virus)	Uncertain	105 × 194 and 105-300	Bacilliform and elongate	Yes	Cytoplasm	Hemocytes, hemopoietic tissue	Johnson and Farley (1980)
HLV (Herpeslike virus)	Herpetoviridae	185 × 214	Icosahedral	Yes	Nucleus	Hemocytes	Johnson (1976b,c)
Baculo-A (Baculovirus-A)	Baculoviridae	70 × 285	Bacilliform	Yes	Nucleus	Epithelium of hepatopancreas	Johnson (1978)
Baculo-B (Baculovirus-B)	Baculoviridae	100 × 335	Bacilliform	Yes	Nucleus	Hemocytes	Johnson, unpubl.

was creamy colored with little texture. Chesapeake Bay virus (CBV), which is related to the Picornaviridae, attacks neurosecretory and other cells of the nervous system and has a predilection for ectodermal tissues (Johnson 1978). Infected crabs show behavioral abnormalities and may be blinded. Signs of CBV disease may be present at least 2 mo before death ensues. Baculovirus A (Baculo-A) does not cause serious disease, although up to 50% of a crab population may be infected (Johnson 1978). Nothing is known regarding pathogenicity of the remaining viruses listed in Table 3. The importance of viral disease in natural populations of the blue crab has not been ascertained. With the exception of HLV and Baculo-A, all information on blue-crab viruses is based on study of captive populations.

Bacterial infections

Shell disease of the blue crab is characterized by the presence of cratered lesions or softened and darkened areas on the exoskeleton. As shell disease progresses, the lesions become confluent (Rosen 1967; Cook and Lofton 1973; Sandifer and Eldridge 1974; Sindermann 1977a). Chitinoclastic species of *Vibrio, Pseudomonas,* and *Beneckea* have been isolated from the lesions (Cook and Lofton 1973). Shell disease is contagious. It occurs in natural populations and may become epizootic in shedding tanks and other artificial enclosures, especially during periods of high water temperatures. It is not fatal, and the cuticle apparently is not completely perforated. However, extensive erosion may lead to secondary invasion of the soft tissues by pathogenic bacteria and fungi. Since molting rids a crab of shell disease, older crabs have a prevalence due to longer intermolt periods.

Hemocoelic bacterial infection is caused by various gram-negative bacteria, often species of *Vibrio* (Krantz et al. 1969; Johnson 1976b, 1977e). Signs of disease are weakness, nonclotting hemolymph, prominent aggregations of hemocytes and bacteria in the gills, and presence of gram-negative bacteria in the hemolymph (Johnson 1976c; 1977e). Hemocoelic bacterial infection may cause extensive mortalities in wounded or otherwise stressed crabs being held in shedding tanks, especially during times of high water temperatures (Johnson 1977e).

Fungal disease of eggs and larvae

Blue crab eggs are attacked and killed by the marine phycomycete, *Lagenidium callinectes* (Couch 1942; Rogers-Talbert 1948; Sindermann 1977b). Zoospores of *L. callinectes* settle on blue crab eggs, germinate on the surface, and extend germ tubes which develop into a branched, septate mycelia (Sindermann 1977b). More than 25% of an egg mass may be destroyed and, in the laboratory, newly hatched larvae can also be killed by *L. callinectes*. Fungal invasion is limited to the periphery of the egg mass. Diseased portions are brownish in yellow to orange egg masses and grayish in the more mature brown to black egg masses. Incidence of infection in natural populations varies from year to year, according to locality, and prevalence may be up to 95% of ovigerous females sampled (Bland and Amerson 1974). *Lagenidium callinectes* is capable of infecting blue crab egg masses in salinities ranging from 5 to 30‰, occurring on the east and gulf coasts of the United States (Sindermann 1977b).

Paramoebiasis

Sprague and Beckett (1966) discovered paramoebiasis (gray crab disease) in blue crabs often characterized by grayish-colored appendages and ventral surface and hemolymph containing amoeboid cells with two nucleuslike bodies having different morphology. Mortalities of 20 to 30% attributed to this disease occurred in several shedding tanks on the lower seaside shore of Maryland (Chincoteague Bay) and Virginia (Wachapreague) in 1965 (Sprague and Beckett 1966). The crabs suffering from the infection were lethargic with grayish-colored appendages and ventral surface. These amoeboid cells were later identified as a *Paramoeba* sp. The amoebae range from 3 to 35 μm and contain a well-defined nucleus and a secondary nucleus (amphosome) which is a major diagnostic character (Couch and Martin 1982). Hepatopancreas, gonad, muscle, gills, and blood are heavily infected during advanced stages of the disease. Newman and Ward (1973) reported that hemolymph smears containing 95 amoebae/100 cells usually occurred in blue crabs exhibiting grayish-colored appendages (Sprague and Beckett 1968). Johnson (1977a) extended the known geographical range of *Paramoeba perniciosa,* detecting the organism only from high salinity areas of Sandy Hook Bay, N.J., and Long Island Sound near Milford, Conn., as well as Chesapeake Bay and Chincoteague Bay. *Paramoeba perniciosa* generally occupies connective tissues and hemal spaces during early stages of infection followed by invasion of hemolymph and replacement of hemocytes (Johnson 1977a, f). Sawyer et al. (1970) reported that paramoebiasis occurs in blue crabs only in salinities > 25‰. Paramoebiasis has not been reported to occur in blue crabs from the gulf coast of the United States (Tatum 1979; Couch and Martin 1982).

Gas bubble disease

Gas bubble disease has been demonstrated in laboratory cultured blue crabs (Johnson 1976a). Intermolt blue crabs (9.5 to 14 cm in width) were held in flow-through systems and exposed to water supersaturated with air resulting in 38% mortality (25 of 66) within the first 2 d after exposure (Johnson 1976a). Exposure to water supersaturated with air caused formation of gas emboli in the hemal system, which caused local ischemia. Hemal spaces of many gill lamellae and stems were filled with gas. Connective tissues were mechanically disrupted by gas bubbles, but ischemic injury was rare. Areas of thickened lamellar epithelia (salt glands) that occur basally on some gills were not affected. Gas bubbles in the heart frequently displaced muscle fibers, causing partial hemal stasis, and blood vessels were often distended by large gas emboli. Johnson (1976a) suggested that focal degeneration of the heart muscle and associated pacemaker nerves may contribute to hemal stasis.

Parasites, egg predator and commensals

Microsporidian infections

A microsporidian protozoan originally referred to as *Nosema michaelis* (Overstreet 1975), and more recently called *Ameson michaelis* (Overstreet 1978), may cause heavy mortalities of blue crabs in natural populations. Infection often occurs when a crab ingests tissues containing spores from an infected crab that is being cannibalized or eaten after death (Overstreet 1975). Vegetative growth occurs in hemocytes located in sinuses in connective tissue surrounding the midgut. According to Weidner (1970) and Overstreet (1975), this is followed by sporogenesis in the sarcoplasm of striated muscle cells and dissolution of infected and adjacent uninfected muscle fibers. Crabs with this so called "sick crab

disease" usually die under any additional stress, such as high water temperature or suboptimal water quality. Gross signs of the disease in the terminal stages include sluggish movement and coarse white appearance and fibrous texture of muscles (Sprague 1965; Overstreet 1977). Preliminary results by Overstreet and Whatley (1975) and Overstreet (1975) indicated that incorporation of Buquinolate (ethyl 4-hydroxy-6, 7-diisobutoxy-3-quinoline-carboxylate) into food offered to blue crabs 48 h before or after infection with *A. michaelis* spores retarded and often terminated "sick crab disease." Oval spores of *A. michaelis* are characteristically 2.2 × 1.7 μm and are known to occur in blue crabs from the Atlantic and Gulf States (Sprague 1965; Sprague and Couch 1971). Also, the closely related microsporidian, *Ameson sapidi* (Overstreet 1978), occurs in muscles of the blue crab in North Carolina waters. The oval spores of this protozoan are 3.5 × 2.1 μm. Biochemical changes in blue crabs infected with *A. michaelis* include: 1) Lactic acid accumulation in the hemolymph, thoracic muscle, and hepatopancreas, 2) increases in most free amino acids (taurine, aspartic acid, threonine, proline, glycine, arginine) detected in the hemolymph except glutamic acid, 3) lower muscle protein content, 4) hypoglycemia (66.3 mg glucose/100 ml hemolymph declining to 51 mg glucose/100 ml hemolymph), and 5) reduced Cl^- and Na^+ ion levels in the blood (Findley et al. 1981).

A *Minchinia*-like haplosporidian was observed in hemolymph from a blue crab from Chincoteague Bay, Va., as well as an individual from Beaufort, N.C. (Newman et al. 1976). Uninucleate cells ranged from 3.4 to 7.3 μm greatest diameter.

Sprague (1966) found the protozoan *Pleistophora cargoi* (= Plistophora) in muscles of an infected male blue crab from the Patuxent River, Md. The spores are ellipsoidal (3.3 by 5.1 μm) and give rise to many spores (32 to 100). Infected host tissues include skeletal and cardiac muscle. The vegetative stages and significance of mortalities of the blue crab in natural populations is unknown.

Nemertean egg predator

The nemertean *Carcinonemertes carcinophila* infests gills and eggs of adult female blue crabs. The nemertean produces a mucus capsule that cements two gill lamellae together (Overstreet 1982). Then, *C. carcinophila* migrates from the gill cavity into the blue crab egg mass, soon after egg extrusion onto the pleopods (Davis 1965). The nemertean feeds on the host's eggs and becomes sexually mature in the blue crab egg mass (Hopkins 1947). Female *C. carcinophila* withdraw from their mucus tubes after mating, leaving their eggs behind while they migrate back to the gills (Pyle and Cronin 1950). Ciliated nemertean larvae hatch and either stay in the mucus tube or swim within the egg mass. Following metamorphosis into a creeping stage, individuals may remain in the original host or infest other crabs (Davis 1965). Large, bright red adult *C. carcinophila* occur on the gills of female blue crabs that have ovulated, serving as a useful indicator of previous spawning (Pyle and Cronin 1950). Hopkins (1947) noted that nemertean infestations of both the sponge and gills were greatest during August and September in blue crabs in Chesapeake Bay following the peak fall spawning period. Infestations of *C. carcinophila* on blue crabs are limited to high salinity regions, therefore gills of male blue crabs are seldom infested.

Parasitic dinoflagellates

Newman and Johnson (1975) found a new disease caused by parasitic dinoflagellates (*Hematodinium* sp.) in blue crabs examined from North Carolina, Georgia, and Florida in 1968 and 1969, whereas individuals from South Carolina did not exhibit the disease. According to Couch and Martin (1982), *Hematodinium* sp. infections have been reported in blue crabs from Maryland to northeastern Gulf of Mexico. Both male and female crabs ranging from 70 to 170 mm carapace width were sampled from salinities of 0 to 36‰. Crabs infected with these parasitic dinoflagellates were only found in salinities > 11‰. In advanced stages, when crabs were moribund, the internal tissues were milky white and the hemolymph was milky white with few, if any, hemocytes. Also, in advanced infections, total lysis of hepatopancreatic tubules and partial destruction of muscle occurs (Couch and Martin 1982). The parasites were unicellular with a mean diameter of 8.1 μm and the cells were nonmotile.

Hyperparasitism in the blue crab

Metacercariae of two digenetic trematodes (*Microphallus basodactylophallus* and *Megalophallus* sp.) being hyperparasitized by the haplosporidian *Urosporidium crescens* have been isolated from blue crab musculature and hepatopancreas (Couch 1974; Overstreet 1978). The metacercariae of the trematode encyst in the blue crab which serves as an intermediate host, with a mammal (e.g., racoon) often serving as a definitive host. Harm is incurred by the blue crab only in the case of very heavy infestations, which cause a localized muscle weakening. Metacercariae of *M. basodactylophallus* infect thoracic muscles, hepatopancreas, and ventral ganglion of blue crabs from Chesapeake Bay to Texas (Overstreet 1982). Uninfected and lightly infected metacercariae are white to cream colored and range from 189 to 269 μm in diameter, whereas infected metacercariae are easily recognized because they become enlarged (410 to 654 μm), darkly pigmented, and easily ruptured. The single layered cyst wall of the metacercariae decreases in thickness from 2.3 to 0.8 μm with heavy infection, and most of the cell parenchyma is replaced by the hyperparasite. Normally, the hyperparasite is released upon death of the blue crab as the metacercarian cell wall ruptures. Couch (1974) suggested that release of the hyperparasites through death of the metacercariae in live blue crabs would probably result in death of *U. crescens* due to destruction by hemocytes or other defense mechanisms of the blue crab.

Metacercariae of the microphallid trematode *Levinseniella capitanea* were isolated from the hepatopancreas and gonads of several adult blue crabs from Cat Island, Miss., (4 of 92 crabs) and 1 of 41 crabs sampled near Raccoon Island, La. (Overstreet and Perry 1972). Hyperparasitism of the metacercariae was not noted.

Peritrichous ciliates

Couch (1966) found two peritrichous ciliates on the gills of blue crabs from Chincoteague Bay and Chesapeake Bay. These crabs were sampled from salinities ranging from 11 to 30‰. The loricate genus *Lagenophrys callinectes* proliferated in high concentrations in the gill lamellae of several crabs in a shedding operation in Franklin City, Va., when water temperatures exceeded 27°C. Once the gill surface was heavily occupied, gill lamellae became fastened together and respiratory current was apparently retarded by *L. callinectes*. Also, the stalked genus *Epistylus* sp. was found in low amounts on the gills of 32 of 41 individuals examined. Although a commensal relationship, Couch (1966) theorized that high density rearing conditions, higher water temperature (i.e., lower oxygen solubility), and an increase of peritrich ciliates may cause anoxia. Couch (1967) later reported that *L. callinectes*

as well as other gill fauna remained on the "old" gill cuticle of blue crabs following ecdysis. However, crabs that had reached their terminal molt no longer have such a mechanism for removing these organisms. Peritrichs feed on bacteria (Sawyer and MacLean 1978) and adhere to the gill lamellae by the lorica (i.e., *Lagenophrys callinectes*) or by a single basal holdfast (i.e., *Epistylis* sp.). These species have not been reported to occur in gulf coast blue crabs (Tatum 1979). *Lagenophrys callinectes* has been reported on some blue crabs sampled from Beaufort, N.C., and Trechard's Inlet, S.C., Maryland, and Virginia waters (Couch 1967).

Barnacles as ectocommensals and parasites

A gooseneck or pedunculate barnacle, *Octolasmis muelleri*, is often found on the efferent side of gills of blue crabs as well as other decapods in high salinity waters (i.e., generally above 15‰). This ectocommensal does not gain nutrition from crabs, but it may interfere with respiration during heavy infestations due to decreased activity of the host's scaphognathite (Walker 1974; Overstreet 1978).

The acorn barnacle, *Chelonibia patula*, is an ectocommensal that often occurs on the carapace of blue crabs, especially those reaching their final postlarval molt. Acorn barnacles on blue crabs have been reported from Delaware Bay (Williams and Porter 1964), South Carolinian waters (Eldridge and Waltz 1977), Mississippi (Overstreet 1978), and St. Johns River, Fla. (Tagatz 1968a).

The cypris larva of the parasitic sacculinid barnacle, *Loxothylacus texanus*, settles on early postmolt juvenile blue crabs and enters into the interior of the crab in toto (Overstreet 1978). Growth of the blue crab is often retarded to a maximum size of 3 to 8 cm carapace width (often called button crabs), thereby making the individual unavailable to the fishery. Most infected crabs appear similar to miniature adult females, with males often transforming secondary sexual characteristics to those of females, possibly as a result of alteration of the androgenic gland. Parasitized males often have 6 distinct abdominal segments, whereas normal males only have 4 abdominal segments (Reinhard 1950). Also, parasitized males have abdominal musculature that is similar to that of females and parasitized females have a broadened abdomen similar to adult females. After formation of an extensive "root system" inside the crab, externae consisting of a brood pouch for larvae and gonads of the parasitic barnacle protrude between the crab's abdomen and thorax. Occurrence of *L. texanus* is rare in low salinity waters (Darnell 1959) and appears to be restricted to gulf coast waters such as Louisiana (Adkins 1972), Mississippi (Perry 1975), and Texas (Reinhard 1950). *Loxothylacus texanus* has not been reported on blue crabs in Chesapeake Bay (Lawler and Van Engel 1973).

A leech (*Myzobdella lugubris* Leidy) occurred on several blue crabs (from Bulow Creek, Volusia County, Fla.) which had suffered recent mortality (Hutton and Sogandares-Bernal 1959). The leeches were located inside the crab near perforations on the carapace and articulations of the pereopods. It is not clear from their report whether the leeches infested the crabs before or after death. Further study indicated that *M. lugubris* derives nutrition primarily from fishes, but uses the carapace of blue crabs as a substrate for its cocoons (Daniels and Sawyer 1975). The cocoons were equally distributed on the posterolateral regions (both dorsal and ventral) of the carapace and occurred on blue crabs from the Ashley River, S.C., (0 to 14‰) from March to November with peak occurrence in October and November.

3.4 Nutrition and growth

3.41 Feeding

Dietary protein concentration requirements of juvenile blue crabs have been examined in several laboratory feeding studies. Juvenile male and female blue crabs (mean initial weight = 1.2 g, mean carapace width = 2.5 cm) achieved better growth when fed 44 or 60% crude protein diets (as percent of dry weight) compared with individuals fed 27% crude protein over a 105-d period (Millikin et al. 1980). Adult, live brine shrimp, *Artemia salina*, fed as reference diet to a separate group of juvenile blue crabs, promoted better growth than any of the laboratory formulated diets. Apparently, there were important nutritional differences other than dietary protein concentration between the high protein (60%) laboratory formula diet and the live brine shrimp diet (58 to 64% crude protein, dry weight). In a separate study, juvenile blue crabs of larger initial size (mean initial weight = 7.8 ± 3.9 g SD, n = 62) gained significantly more weight per molt on a 5-d postmolt basis when fed 25 or 40% crude protein than when fed 15% crude protein (Fortner[6]). Therefore, laboratory reared juvenile blue crabs ranging from approximately 1 to 10 g (25 to 55 mm carapace width) require a minimum of 40% dietary protein in terms of growth rate, while slightly larger juvenile blue crabs require dietary protein concentrations of 25% or more, but < 40%. Winget et al. (1976) reported no significant differences in growth of juvenile blue crabs (initial mean carapace width = 59 mm) fed 26, 46, 62, or 75% crude protein on a dry weight basis over a 60-d period. However, growth differences in the previously described protein requirement studies (Millikin et al. 1980; Fortner footnote 6) were not observed until after 105 and 63 d, respectively. Therefore, a longer experimental period by Winget et al. (1976) possibly would have demonstrated differential growth due to dietary protein concentration.

Salinity is not an important factor governing food conversion in laboratory reared juvenile blue crabs. Holland et al. (1971) reported that juvenile blue crabs (initial weight = 0.2 to 0.4 g) had similar food conversion rates regardless of salinities ranging from 6 to 21‰.

Blue crabs require an exogenous source of sterol. Whitney (1970) demonstrated that juvenile and adult blue crabs at intermolt, premolt, and soft shell stages were incapable of synthesizing either squalene or sterols from acetate-1-^{14}C, or mevalonate-2-^{14}C.

Biddle et al. (1978) concluded that 3 or 9% dietary fiber (dry weight basis) was satisfactory for juvenile blue crabs of two size groups (2.5 to 6.0 g and 6.1 to 36.4 g initial weight) in terms of survival, growth, and food conversion over a 9-wk period. However, crabs fed diets containing 27% fiber had increased mortality due to a Herpeslike virus. Also, crabs fed 27% dietary fiber had poorer food conversion ratios and greater feed intake, possibly due to less availability of nutrients per unit weight of food ingested.

Glycogen content of the hepatopancreas of blue crabs has been evaluated according to molt stage, season, and sex. Blue crabs (5 to 15 cm carapace width) sampled from Delaware Bay had highest

[6]A. R. Fortner, Southeast Fisheries Center Charleston Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 12607, Charleston, SC 29412, pers. commun. September 1982.

hepatopancreatic glycogen concentration (8.1 mg/g tissue) during premolt (stage D), followed by 6.6 mg glycogen/g hepatopancreas (midgut gland) during soft shell stage (stage A), and approximately 3.0 mg glycogen/g tissue during early postmolt (stage B) and intermolt (stage C) (Rouse 1972). Glycogen concentrations of the hepatopancreas were significantly lower in summer, with highest concentrations during winter and decreasing concentrations during spring. Also, hepatopancreatic glycogen concentrations were higher for females in molt stages A, B, and D than comparative stages in males. Lower hepatopancreatic glycogen concentrations for females than males in stage C might be the result of mobilization of glycogen reserves to aid in production of ova (Rouse 1972). Midgut gland glycogen content appears to have an annual cycle in blue crabs, according to a study from Indian River Bay, Del. (Winget et al. 1977). Crabs ranging from 11 to 150 g, had 8.4 mg glycogen/g tissue during November-December, 10.4 mg during February-March, 5.3 mg during April, and 3.3 mg during June-September (Winget et al. 1977). Sampling during each season for several years is necessary to verify these preliminary results.

Mean whole body protein values of intermolt juvenile blue crabs 3 to 7 cm carapace width ranged from $34.7 \pm 0.27\%$ (SE) on a dry weight basis for individuals fed 27% dietary crude protein over 18 wk to approximately 40% whole body protein for crabs fed 44 or 60% dietary crude protein (Millikin et al. 1980). Crabs fed adult brine shrimp over the same time interval had significantly higher whole body protein ($46.1 \pm 1.8\%$) than individuals fed the laboratory formula diets containing 27, 44, or 60% crude protein. Whole body glucosamine values were approximately 4% on a dry weight basis for juvenile blue crabs regardless of dietary treatment (Millikin et al. 1980).

Ash composition of juvenile blue crabs reared in the laboratory that were from 8 d postmolt to late premolt stage (3 to 7 cm carapace width) consisted of 30 to 40% of total, whole-body dry matter, while calcium was 9 to 13% of whole body dry matter and phosphorus was 0.7 to 1.5% of whole body dry matter (Millikin unpubl. data). Whole-body dry matter of juveniles 8 d postmolt to late premolt ranged from 20 to 32%. Blue crabs that were 2 to 6 d postmolt generally had lower whole body ash as a percent of dry matter (24-28%), lower calcium as a percent of dry matter (5 to 6%), lower whole-body dry matter content (17 to 20%), and similar phosphorus concentrations as a percentage of dry matter (1.3 to 1.4%).

3.42 Food

Data are scarce on food organisms consumed by larval stages of the blue crab in natural waters. Although phytoplankton may be consumed, plant material alone is believed to be deficient in protein content (Costlow and Sastry 1966). Various phytoplankton species fed to early zoeal stages in the laboratory without concurrent feeding of zooplankton, prolonged time before death compared with survival time of starved larvae (Costlow and Bookhout 1959), but unicellular algae fed alone did not result in successful molting of first stage zoeae to second stage zoeae. According to Sulkin and Epifanio (1975) and Sulkin (1978), rotifers, *Brachionus plicatilis,* ranging from 45 to 80 μm, promote high survival and molting success during the first 14 d of development, whereas recently hatched nauplii of *Artemia salina* (250 μm) fed alone to first and second stage zoeae produce low survival and molting success (Costlow and Bookhout 1959). Therefore, zooplankton in the size range of 45 to 80 μm probably are among the chief sources of food organisms for blue crab larvae, especially in the early stages.

Juvenile and adult stages of blue crabs feed chiefly upon molluscs, crustaceans, and fish. According to Tagatz (1968a), crustaceans and molluscs are the chief food items of juvenile blue crabs < 21 mm carapace width. Juveniles larger than 21 mm carapace width fed primarily upon clams, fish, and crustaceans. Jaworski (1972) reported that crustaceans and molluscs are equally important in terms of percentage stomach volume in blue crabs between 30 and 74 mm carapace width. Molluscs comprised an appreciably greater stomach volume than crustaceans in crabs > 125 mm carapace width (Jaworski 1972). Laughlin (1982) divided blue crabs from Apalachicola Bay into three trophic groups based upon stomach contents. Smallest juveniles (< 31 mm carapace width) fed mainly upon bivalves, plant matter, ostracods, and detritus. The second trophic group (31 to 60 mm carapace width) consumed mostly fishes, gastropods, and xanthid crabs, while the third trophic group of blue crabs (> 60 mm carapace width) fed on bivalves, fishes, xanthid crabs, and blue crabs. Van Engel (1958) listed occurrence of several food items in juvenile and adult blue crabs, such as fresh and decaying fish; juvenile oysters (*Crassostrea virginica*); hard clams, *Mercenaria mercenaria*; sea lettuce, *Ulva* sp.; roots, shoots, and leaves of eelgrass; and salt marsh grass, *Spartina alterniflora*. The coot clam, *Mulinia lateralis,* is an important prey item of blue crabs in the York River, Va., estuary (Virnstein 1977). Other food items of blue crabs include small oysters (Menzel and Hopkins 1956; Menzel and Nichy 1958), three species of mussels: *Congeria leucophaeta, Mytilopsis leucopheata,* and *Brachidontes exustus* (Darnell 1961; Odum and Heald 1972), the soft shell clam, *Mya arenaria* (Dunnington 1956), and the wedge clam, *Rangia cuneata* (Darnell 1961). Hamilton (1976) observed predation by juvenile blue crabs (25 to 65 mm carapace length) on marsh periwinkles, *Littorina irrorata* (9 to 15 mm shell length). Laboratory studies indicated that juvenile blue crabs ranging from 10 to 15 cm carapace width consumed cultchless oyster (*C. virginica*) up to 4 cm shell length, while blue crabs from 65 to 80 mm carapace width could not feed upon oysters > 25 mm shell length (Krantz and Chamberlin 1978). Large blue crabs (15 to 16 cm) consumed Atlantic ribbed mussel, *Geukensia* (= *Modiolus*) *demissa,* < 8 cm shell length (Seed 1980). Medium-sized crabs (10 to 11 cm) and small crabs (6 to 7 cm) consumed Atlantic ribbed mussels up to 5.5 and 4.8 cm, respectively, in the laboratory. Blue crabs > 80 mm carapace width were capable of breaking open the largest *Mya arenaria* shells (90 mm dorsoventral axis) tested according to compression measurements of chelae force at the dactyl tip (Blundon and Kennedy 1982a). The same investigators reported that only large (> 40 mm shell height) wedge clams were capable of withstanding crushing capabilities of large blue crabs (100 to 165 mm carapace width). In a separate study, *M. arenaria* (30 to 40 mm shell length) buried at either 5, 10, 15, or 20 cm were consumed less frequently at either 15 or 20 cm depths than at 5 or 10 cm depths by large blue crabs (121 to 180 mm carapace width) (Blundon and Kennedy 1982b).

3.43 Growth and morphometry

Growth of blue crabs is dependent upon temperature, molting frequency, food availability and nutritional quality, and life stage of the individual. Growth primarily occurs during molting, although small weight increases occur through relative changes in tissue content during the intermolt period (relative increases

of whole body protein compared with moisture). Generally, as temperature decreases, food consumption rate decreases, especially between 34° and 13°C (Leffler 1972). Tagatz (1968b) observed that growth per molt of blue crabs remained similar regardless of temperature (summer vs. winter) in the St. Johns River, Fla., but that intermolt intervals were three to four times longer in winter. Therefore, low temperatures that prevent molting altogether or increase intervals between molts significantly reduce growth rate. Churchill (1921) reported that females cease feeding activity in Chesapeake Bay below 10°C. According to Van Engel et al. (1973), growth occurs in blue crabs in Chesapeake Bay from late April to mid-October when temperatures are generally above 15°C and blue crabs undergo semihibernation when temperatures fall to 5°C or less.

Salinity values ranging from 6 to 30‰ do not differentially affect growth of juvenile and adult blue crabs. Growth of female crabs during and following their terminal molt was not differentially affected by salinities of 9, 16, or 27‰ (Haefner and Shuster 1964) or 10, 20, or 30‰ (Haefner 1964). Holland et al. (1971) reported that salinities ranging from 6 to 21‰ (6, 11, 16, or 21‰) did not affect growth or food conversion of laboratory reared juvenile crabs (5 to 40 mm carapace width).

Growth rate of juvenile blue crabs up to at least 7 cm carapace width does not vary between sexes. Only one of eight groups of 40 juveniles of equal age fed various diets over an 18-wk period showed differential growth between sexes (Millikin et al. 1980). Size variation of the first seven juvenile instars reared in the laboratory is described in Table 4 (Newcombe, Sandoz, and Rogers-Talbert 1949).

Table 4.—Size variation of first seven juvenile stages of blue crabs.[1]

Juvenile instar	Carapace width (range—mm)	Mean carapace width (mm)	SD
1	2.2 to 3.0	2.5	0.14
2	3.0 to 4.2	3.7	0.25
3	4.1 to 6.0	5.1	0.42
4	5.5 to 7.4	6.6	0.46
5	7.2 to 10.0	8.6	0.66
6	8.7 to 12.4	10.2	0.85
7	9.7 to 13.0	11.0	0.81

[1] $N = 50$ for first 6 instars, $N = 35$ for seventh instar (Newcombe, Sandoz, and Rogers-Talbert 1949).

After early juvenile stages, considerable overlap in sizes between instars occurs. Tagatz (1968a) reported that fully grown crabs range from 100 to 240 mm carapace width. Tyler and Cargo (1963) showed considerable overlap in carapace width between the penultimate instar (81 to 135 mm, $N = 254$) and the ultimate instar (118 to 195 mm, $N = 88$) for females from several sampling sites of Chesapeake Bay. Tagatz (1968b) reported mean carapace widths and ranges for adult males (mean = 147 mm, ranging from 117 to 181 mm), mature females (mean = 148 mm, ranging from 128 to 182 mm), immature females (mean = 111 mm, ranging from 100 to 130 mm), and ovigerous females (mean = 152 mm, ranging from 116 to 180 mm). Tagatz (1968b) also found a considerable range between the smallest mature female (99 mm carapace width) and the largest immature female (177 mm carapace width) sampled from St. Johns River, Fla. Tagatz (1965) reported a maximum carapace width for males sampled from commercial catches in St. Johns River to be 246 mm carapace width, while the heaviest male (225 mm carapace width) weighed 550 g. Van Engel et al. (1973) reported a maximum size for male blue crabs from Virginia as 241 mm carapace width. The largest immature female sampled from commercial catches during a 3-yr period from five estuaries in South Carolina was 154 mm carapace width (Eldridge and Waltz 1977).

Variation of growth increments per molt ((postmolt weight − premolt weight) ÷ (premolt weight) × 100) may be largely the result of both dietary nutritional quality and temperature. Tagatz (1968b) reported that temperatures between winter (15°C) and summer (25° to 30°C) in St. Johns River were not reflected in significant seasonal alteration in growth increments of blue crabs. However, Leffler (1972) reported that blue crabs of 20 to 69 mm carapace width, demonstrated an average increase in growth per molt as temperature decreased from 34° to 15°C. Juvenile blue crabs ranging in initial weight from 3.5 to 23.7 g increased $33 \pm 8.4\%$ ($n = 18$) in weight when fed a 15% crude protein diet, $51.9 \pm 9.6\%$ ($n = 19$) increase in weight when fed a 25% crude protein diet, and $57.6 \pm 12.2\%$ ($n = 23$) increase in weight when fed a 40% crude protein diet for individuals weighed on a 5-d postmolt basis in the laboratory (Fortner footnote 6).

Growth per molt of blue crabs is highly variable in natural waters. Growth increments per molt in terms of carapace width varied from 7.8 to 50% in juvenile and adult blue crabs held in floating tanks in St. Johns River (Tagatz 1968b). Percent growth increase averaged 32% for females during their terminal molt. Mean percent increments in growth in 10 mm width intervals varied from 21 to 34% for crabs from St. Johns River (Tagatz 1968b). Mean percent increments in carapace width ranged from 11.9% for small juvenile females (10 to 19.9 mm) to 33.7% for large females (100 to 109.9 mm) while mean percent increments ranged from 14.4% for small juvenile males (10 to 19.9 mm) to 32.9% for males ranging from 80 to 89.9 mm carapace width (Gray and Newcombe 1938b). Growth per molt (percent increase in carapace width) during the terminal molt of females from St. Johns River averaged 34.4% ($n = 85$) in salinities > 5‰ and 30.2% ($n = 85$) in salinities < 1‰ (Tagatz 1968b). Average values of growth per molt (percent increase in length) during the terminal molt of females from three sampling sites in Chesapeake Bay ranged from 23.4 to 25.6% (Haefner and Shuster 1964).

Average size (carapace width) at maturity for females was appreciably smaller for Chincoteague Bay crabs (5.3 in = 13.5 cm) compared with Delaware Bay crabs (6.3 in = 16 cm) and Chesapeake Bay crabs (6.5 in = 16.5 cm) (Porter 1955).

Autotomy and regeneration of appendages are common among many crustacean species (Weis 1976), including blue crabs. If an appendage is firmly imprisoned or seriously injured, a break occurs along a fracture plane located on the distal end of the basis, with eventual replacement of the appendage by regeneration (Pyle and Cronin 1950). The regenerating limbs grow in a folded position and are often functional following the next molt (Weis 1976). Laboratory studies showed that mortality among blue crab megalopae was low when chelae were induced to autotomize, compared with megalopae with chelae cut at a site other than the basi-ischiopodite fracture plane (Costlow 1963a). If the chelae were lost prior to day 4 of the megalopal intermolt period, then the completely regenerated appendage normally appeared at metamorphosis. Although 100% of hatchery-raised crabs had a right "crusher" cheliped (larger) and a left "cutter" cheliped, only 79% of 1,156 crabs sampled from natural waters showed the same morphological character (Hamilton et al. 1976). A trend existed for larger crabs to have a larger percent occurrence of a left "crusher" cheliped and right "cutter" cheliped, which Hamilton et al. (1976) felt to be due to reversed cheliped laterality through autotomy and regeneration. Shuster et al. (1963) attributed most of the bizarre

claw deformities of blue crabs sampled from the field to new growth in the form of duplication at the site of injury rather than autotomy followed by regeneration.

Male blue crabs are generally heavier than female blue crabs for a given carapace width. Pullen and Trent (1970) reported carapace width-total weight relations for crabs from Galveston Bay, Tex., > 25 mm carapace width, excluding gravid females: Male crabs (log weight = −3.74 + 2.775 log carapace width) and female crabs (log weight = −3.54 + 2.639 log carapace width). Newcombe, Campbell, and Eckstine (1949) reported carapace width-total weight relationships for blue crabs from Chesapeake Bay (Virginia portion) using untransformed data as follows: Male crabs (weight = 0.00026 width$^{2.67}$) and female crabs (weight = 0.00034 width$^{2.57}$). A graphic presentation of carapace width vs. weight also demonstrated that male blue crabs are generally heavier than females from St. Johns River for a given carapace width between 100 and 200 mm (Tagatz 1965).

Length to width ratio (in the form of a percentage) steadily decreases as carapace width increases in blue crabs. Tagatz (1968b) reported values of 50% for males and females from St. Johns River between 10 and 19 mm carapace width and 40.7% for males and 38.8% for females for individuals between 140 and 149 mm carapace width. Newcombe, Sandoz, and Rogers-Talbert (1949) reported values equivalent to length:width ratio as a percentage as being 53.2% for males and 53.9% for females from Chesapeake Bay between 10 and 19 mm carapace width. Carapace length was 44.9% of carapace width for males and 41.7% for females from Chesapeake Bay between 140 and 149 mm carapace width.

Mature males from Ashley River, S.C., had a greater average weight than immature males having the same carapace width, while immature females were heavier than mature females for a given carapace width (Olmi and Bishop 1983). According to Olmi and Bishop (1983), the lighter weight of adult females compared with immature females of the same carapace width, may result from the maturity molt transformation of females into long spined forms as observed by Tagatz (1965) and Gray and Newcombe (1938a).

Due to the problem of variation in lateral spine lengths for a given size crab (e.g., carapace length or width at the base of the spine), Olmi and Bishop (1983) suggested that measurement of carapace length or width at the base of the lateral spines might be more accurate in developing a regression analysis with closer agreement between observed and predicted values of body weight. Carapace length was originally suggested by Gray and Newcombe (1938a) as an alternative to carapace width for prediction of body weight, whereas Williams (1974) suggested the use of carapace width at the base of the lateral spines (rather than from tip to tip) to predict body weight.

3.44 Metabolism

Oxygen consumption in blue crabs is a function of size, temperature, and molt cycle. Leffler (1972) reported greater increases in standard metabolic rate in blue crabs (20 to 69 mm carapace width) reared in 34° vs. 27°C compared with crabs reared in 27° vs. 20°C. Oxygen consumption increases as temperature increases from 10° to 25°C (Laird and Haefner 1976). Lewis and Haefner (1976) demonstrated that premolt female blue crabs in the penultimate instar had higher oxygen consumption rates (μl O_2/g wet weight per h) than molting or postmolting crabs. Twelve hours or less after completion of molting, weight-specific oxygen consumption was depressed, whereas oxygen uptake increased after 12 h. Also, total oxygen consumption increased with higher wet weights of females in the terminal molt stage, but weight-specific oxygen consumption decreased as total wet weight of the blue crabs increased (Lewis and Haefner 1976). Laird and Haefner (1976) also found that oxygen uptake decreased with increases of total wet weight of blue crabs. Oxygen uptake evaluated in a 3 × 3 factorial (10°, 17°, and 25°C; 10, 20, and 30‰ salinities) resulted in no differences in oxygen consumption between sexes (Laird and Haefner 1976). Lower average oxygen consumption occurred at a salinity of 20‰ than at 10‰. Also, blue crabs acclimated to cold temperatures (10°C) had a higher mean oxygen uptake when acclimated to a salinity of 10‰ than when acclimated to a salinity of 30‰.

Oxygen consumption rates generally increase as salinity decreases. King (1965) showed that oxygen consumption increased 53% in juvenile blue crabs reared in salinities of 7 to 9‰ compared with crabs reared in full strength seawater, regardless of the salinity from which the experimental animals were captured. Excised gills from adult blue crabs demonstrated higher respiration rates when crabs were reared in 300 mOsm seawater than individuals reared in 940 mOsm seawater (Cantelmo and Ranga Rao 1978). Furthermore, Findley et al. (1978) demonstrated that adult blue crab respiration was significantly higher at salinities of 10 and 20‰ than at 30‰. Oxygen consumption rates decreased with increase in salinity from 5 to 35‰ among adult male and female crabs and immature crabs during winter (Engel and Eggert 1974).

The mixed function oxygenase, arylhydrocarbon hydroxylase, was shown to have highest specific activity in the pyloric stomach and antennal gland (green gland) of males and females (Singer and Lee 1977). Since mixed function oxygenases function in the metabolism of bile acids, fatty acids, and steroid hormones as well as hydroxylation of the aromatic ring of petroleum hydrocarbons, the authors suggested that exposure to sublethal concentrations of petroleum could conceivably interfere with metabolism related to molting (i.e., growth).

3.45 Molting

Stages of the molt cycle of the blue crab were described by Johnson (1980) as modified from Passano (1960) as shown in Table 5.

Intermolt periods increase with age of blue crabs, but are generally shortened by ample food availability, high dietary nutrient quality, and higher water temperatures. Based upon laboratory studies, blue crabs are believed to molt 8 times (seven zoeal stages plus a megalopal stage) (Costlow and Bookhout 1959), followed by as many as 18 to 20 postlarval molts for females and 21 to 23 postlarval molts for males (Van Engel 1958). Blue crabs ranging in carapace width from 10 to 160 mm attained maximum expansion of their new exoskeleton within 6 h following molting (Gray and Newcombe 1938b). Graham and Beaven (1942) suggested that blue crabs cease molting when temperatures are depressed to about 16°C from approximately November to the middle of April in Chesapeake Bay. Ecdysis has been observed at temperatures as low as 3.8°C in blue crabs from St. Johns River, Fla. (Tagatz 1968b). Leffler (1972) observed appreciably shorter intermolt intervals for blue crabs (20 to 69 mm carapace width) reared at 27° or 34°C than individuals reared at 13°C. However, growth per molt frequently decreased as intermolt period decreased. Similarly, blue crabs molted more frequently at 30°C than at 20°C, but growth per molt was greater at 20°C (Winget et

Table 5.—Molt cycle stages of the blue crab, *Callinectes sapidus* (from Johnson 1980).

Stage	Name	Characteristic
Stage A		
A_1	Newly molted	Continued water absorption and initial mineralization
A_2	Soft	Exocuticle mineralization
Stage B	Papershell	
B_1		Endocuticle secretion begins
B_2		Active endocuticle formation, chelae hard; tissue growth begins
Stage C	Hard	
C_1		Main tissue growth
C_2		Tissue growth continues
C_3		Completion of exoskeleton; membranous layer formed
C_4		"Intermolt"; major accumulation of organic reserves
or		
C_4T	Permanent anecdysis	Terminal stage in adult female; no further growth
Stage D	Proecdysis	
D_0		Epidermal and hepatopancreas activation
D_1		Epicuticle formed and spine formation begins
D_2	Peeler	Exocuticle secretion begins
D_3		Major portion of skeletal resorption
D_4	About to molt	Ecdysial sutures open
Stage E	Molt	Rapid water uptake and exuviation

al. 1976). Molting frequency of juvenile blue crabs was greater when individuals were fed live, adult brine shrimp, *Artemia salina,* than when fed laboratory formula diets over an 18-wk period (Millikin et al. 1980). Importantly, limited data from the same study indicated that growth per molt did not decline in blue crabs that molted more frequently.

Intermolt periods during early juvenile development of blue crabs that occurred in the laboratory are listed in Table 6 (Millikin unpubl. data). Mean duration of the first and second crab stage was longer in a salinity of 25‰ and 23.5 ± 1.5°C (Millikin unpubl. data) than in studies conducted at a salinity of 30‰ and 25°C (Rosenberg and Costlow 1976; McKenney and Costlow 1981). Mean duration of the first crab stage in control groups was 3.0 ± 0.4 d (SD) or 4.5 ± 0.25 d (SE) (Rosenberg and Costlow 1976; McKenney and Costlow 1981).

Female blue crabs rarely, if ever successfully, molt again following their maturity molt (terminal molt) (Churchill 1921; Van Engel 1958). An adult female in the process of molting (buster stage) was reported by Abbe (1974) and four different mature females in the buster stage have been observed by Cronin[7]. Olmi and Bishop (in press) reported capture of an adult female in proecdysis (pink sign) that consequently died during ecdysis in the laboratory.

The absolute amount of calcium in blue crabs (size not reported) increased steadily in individuals up to at least 10 d postmolt with a 2.5-fold increase in total protein and a 4-fold increase in chitin in the cuticle from ecdysis to 10 d postmolt (Vigh and Dendinger 1982).

[7]L. E. Cronin, Chesapeake Research Consortium, Shadyside, MD 20764, pers. commun. August 1982 and March 1983.

Table 6.—Intermolt periods during early juvenile development of blue crabs reared individually in the laboratory.[1]

Instar numbers of juvenile stage	Mean intermolt period (d)[2]	Instar numbers of juvenile stage	Mean intermolt period (d)
1-2	7.2 ± 2.7 (104)	8-9	16.6 ± 4.6 (156)
2-3	7.6 ± 3.0 (157)	9-10	19.7 ± 7.1 (143)
3-4	8.0 ± 2.5 (157)	10-11	22.9 ± 8.0 (119)
4-5	9.2 ± 3.8 (157)	11-12	27.6 ± 7.7 (75)
5-6	11.1 ± 4.2 (157)	12-13	27.7 ± 7.1 (38)
6-7	12.6 ± 2.8 (157)	13-14	27.7 ± 6.1 (32)
7-8	14.7 ± 5.1 (156)		

[1]Temperature = 23.5 ± 1.5°C, salinity = 25‰ with gradual reduction to 20‰ after 160 d, photoperiod = 8 h light/16 h dark. (Millikin, unpubl. results.)

[2]Mean ± standard deviation of number of days between molt instars of juvenile development. Number of crabs for each intermolt period are in parentheses.

3.5 Behavior

3.51 Migrations and local movements

After hatching and larval development of blue crabs in high salinity waters (Costlow and Bookhout 1959; Costlow 1967), megalopae are recruited into estuarine waters (Boicourt 1982; Sulkin and Van Heukelem 1982) followed by migration of early juvenile stages of both sexes upstream to lower salinity waters (Van Engel 1958). Early juvenile stages feed in shallow waters (Van Engel 1958; Tagatz 1968a; Jaworski 1972). During fall migrations in Chesapeake Bay, concentrations of females in the Virginia portion of the Bay occur in deep channels, while males generally overwinter in lower salinity waters, with larger males occurring in deeper waters than smaller males (Van Engel 1958). Especially in spring, immature females approaching their terminal molt migrate to lower salinity waters to seek out mature males for mating. Soon after mating, females initiate migrations back to higher salinity waters that are favorable for larval development. This pattern of migration has been observed in many geographical regions, such as Delaware Bay (Cronin 1954), Chesapeake Bay (Van Engel 1958), Newport and White Oak Rivers, N.C. (Judy and Dudley 1970), South Carolina (Eldridge and Waltz 1977), Barataria estuary, La. (Jaworski 1972), Lake Pontchartrain, La. (Darnell 1959), Mobile Bay (Tatum 1979), Mississippi Sound (Perry 1975), and to some degree in St. Johns River, Fla. (Tagatz 1968a). Migration of adult females along the gulf coast of Florida is generally in a northward direction alongshore following mating (Oesterling 1976). Most tagged adult males that were recaptured had remained in the estuary of initial capture. Adult blue crabs do not migrate appreciably between adjacent estuaries in South Carolina (Fischler and Warburg 1962).

Most migrations of adult female crabs were southward from four release sites within Delaware-Maryland-Virginia seaside bays (north to south: Assawoman Bay, Isle of Wight, Sinepuxent Bay, and Chincoteague Bay, Maryland and Virginia) (Cargo 1958). This occurred despite lack of a continuous increase in salinity from north to south across several inlets (Cargo 1958).

Several studies have been conducted to determine optimal tagging methods for tracking movements of juvenile and adult blue crabs. Cronin (1949) reported that Nesbit-type tags wired across the carapace and looped over the lateral spines of adult blue crabs were a better technique for tracking movements than are tags placed in the branchial chamber through a slit in the carapace, external tags inserted into slots on the carapace, or a Nesbit modification of a Petersen tag on the lateral spine. Fannaly (1978) reported high rates of retention of a spaghetti-type tag by juvenile and adult blue crabs (80 to 150 mm carapace width) following molting in the laboratory. The tag consisted of a monofilament leader (30 mm) and anchor to which plastic tubing was connected. The tags were inserted through the thick membrane at the dorsoposterior articulation of the fifth pereopod.

Blue crabs frequently move inshore during rising tide, forage in the intertidal zone, and move offshore during ebb tide (Nishimoto and Herrnkind 1978). According to both field and wave tank experiments on "eye-capped" individuals, blue crabs are capable of using the beach slope and wave surge for directional orientation.

3.52 Schooling

According to Van Engel (1958), schools of adult female crabs have been observed migrating downstream in tributaries of the Chesapeake Bay. Also, schools of "sea run" or "ocean" crabs appear in late July or early August in the Lynnhaven Roads area (Virginia), consisting of older, adult females with carapaces heavily encrusted with barnacles (Van Engel 1958). However, it is more accurate to describe these groups as aggregations rather than schools (see Partridge 1982).

3.53 Responses to chemical stimuli

Detection of seawater solutions of freeze-dried clam extract by blue crabs was assessed by noting rates of antennular flicking and gill bailing activity (Pearson and Olla 1977). Blue crabs detected the extract solution at 10^{-15} g/l, while feeding behaviors were elicited at concentrations of 10^{-1} to 10^{-2} g/l. Blue crabs were reported to detect naphthalene concentrations of 0.12 mg/l (Pearson and Olla 1979). Further study revealed that the threshold concentration at which 50% of the crabs detected naphthalene was 8.5×10^{-8} mg/l (Pearson and Olla 1980). Lack of information regarding toxicity of naphthalene to blue crabs, especially sublethal effects, prevents comparison of detection threshold concentrations with concentrations which may be toxic.

4 POPULATION

Blue crab populations or stocks in the fishery management context have not been adequately defined for adjacent estuarine areas along the Atlantic coast or gulf coast of the United States. Recently, a workshop was convened to attempt to develop methods for analysis of local blue crab stocks, particularly in Chesapeake Bay (Cronin footnote 7). Results of this workshop are not yet available. Miller et al. (1975) suggested as a result of a 2-yr sampling study that the Chesapeake and Delaware Canal provides little, if any, access for crab migration from Delaware Bay westward to upper Chesapeake Bay. Cole and Morgan (1978a) suggested that observed genetic similarity (gene frequencies of polymorphic enzymes, percentages of polymorphic enzymes, and average heterozygosity) between Chesapeake Bay and Chincoteague Bay populations is the result of larval intermixing of zoeae just outside Chesapeake Bay. However, Porter (1955) reported that adult female crabs in Chincoteague Bay are significantly smaller than those in either Delaware or Chesapeake Bay populations. Possibly, adult females that occur in the Chincoteague Bay are smaller from spending more of their life cycle in waters containing less available food.

4.1 Structure

4.11 Sex ratios

Sex ratios of adult blue crabs differ spatially with respect to salinity, and temporally with respect to peak occurrence of mating, and female migrations to high salinities for spawning. Truitt (1939) reported that 64% of all (adult) crabs captured in the Capes section (Cape Charles to Cape Henry, Va.) of Chesapeake Bay during June and July were egg-bearing females. Crabs taken from areas below the York River and Cape Charles averaged about 9.8% males over a 1-yr period, whereas males may reach 90% of the total adult population in headwaters of the Maryland portion of Chesapeake Bay. Sex ratios (male to female) for crabs sampled in the Chesapeake and Delaware Canal combined with immediately adjacent waters in Chesapeake Bay and Delaware Bay (in salinities of 0.6 to 2.3‰) ranged from 1.0 (June 1972) to 5.8 (August 1971) for recruitment stage classification (1-59 mm carapace width), 0.4 (June 1972) to 4.7 (September 1971) for growth stage classification (60 to 119 mm carapace width), and 1.9 (August 1971) to 16.0 (August 1972) for mature stage (> 120 mm carapace width) (Miller et al. 1975). Much lower male to female sex ratios varied from 0.3 to 1.8 for crabs sampled by the same methods in Tangier Sound, Md., a higher salinity area than the Chesapeake and Delaware Canal and adjacent waters (Miller et al. 1975). Tagatz (1968a) reported that 60 to 90% of crabs sampled in the lower 24 km of the St. Johns River, Fla., from January through September, were females while only 10 to 25% of crabs sampled from October through December were female. In the next 24 km upstream, 75% of the crabs sampled from December through February were females, whereas from March through November 15 to 55% were females. Males dominated the lower salinity areas (farther upstream than 48 km from the mouth of the river). According to Eldridge and Waltz (1977), incidental crab catch contained 84% females during shrimp trawling operations conducted primarily during winter in high salinity areas (e.g., sounds) within 0.8 to 4.8 km offshore of South Carolina. Crab pot catches, which are primarily in lower salinity waters, contained 72% males and 28% females in southern estuaries of South Carolina (Eldridge and Waltz 1977). Van Engel[8] reported that 85 to 95% of the winter dredge crab fishery of Virginia is adult females.

4.13 Size composition

Tagatz (1965) monitored size composition of commercial catches of the St. Johns River, Fla. (80 samples from crab pot catches yielding 11,620 individuals and 12 samples from trawl catches yielding 1,655 individuals). The modal 10 mm carapace width interval for both gear types was 160 to 169 mm. Mean carapace widths from three different areas along the St. Johns River ranged from 155 to 166 mm.

Mean carapace widths of males from commercial crab pot catches from five estuaries in South Carolina ranged from 135.5 to 137.9 mm, while mean carapace widths of females ranged from 148 to 154 mm (Eldridge and Waltz 1977).

4.2 Abundance and density (of population)

4.22 Changes in abundance

Variations in abundance of blue crabs can be estimated to some extent by examining fluctuations of annual commercial catches, although factors other than abundance such as demand and ex-vessel price also affect blue crab landings. Among many factors that cause wide fluctuations in annual population sizes of blue crabs are: 1) Maturation at an early age (1 to 2 yr), 2) short life span

[8]W. A. Van Engel, Virginia Institute of Marine Science, Gloucester Point, VA 23062, pers. commun. August 1982.

(3 to 4 yr), and 3) natural catastrophes that may cause higher than average mortality rates during hatching or winter (Dintaman[9]).

In the mid-1930's, the decline of the Rhode Island blue crab fishery began (Jeffries 1966). By the early 1940's, commercial landings were no longer recorded (Table 6).

In a 3-yr sampling study in Core Sound, N.C., juvenile crabs $\leq$ 4 cm reached greatest numbers between December and April in creeks, followed by migrations to deeper waters, causing low annual amounts of this size range in May (Dudley and Judy 1973). These authors proposed using the mean catch of juvenile blue crabs from creeks in this area as an annual index of juvenile abundance and predictive measure for subsequent adult abundance.

4.24 Changes in density

Miller et al. (1975) reported catch density values (number of crabs/$m^2 \times 10^{-3}$) of three size classes of crabs (recruitment: 1-59 mm carapace width, growth: 60-119 mm carapace width, and mature: $\geq$ 120 mm carapace width) in Delaware Bay and Chesapeake Bay (Elk River) near the Chesapeake and Delaware Canal, the Chesapeake and Delaware Canal itself, and Tangier Sound. For "recruitment size," values changed from 1.27 in June, to 0.88 in August, to 0.28 in September in the Elk River, and 0.55 in June, to 0.08 in August, to 0.07 in September in upper Delaware Bay. For the "growth" size class, catch density values varied from 1.99 in June, to 2.49 in August, to 1.04 in September in the Elk River and from 0.65 in June, to 1.56 in August, to 0.16 in September in upper Delaware Bay. Catch density values were at least two to three times greater for crabs in each size class in Tangier Sound than in the Elk River sampling area for similar sampling periods. Also, catch density values in the Chesapeake and Delaware Canal were 0.8 or lower for the growth size class, 0.1 or lower for the recruitment size class, and 0.3 or lower for the mature size class.

4.3 Natality and recruitment

4.33 Recruitment

Time to recruitment to blue crab fisheries varies according to geographical region, mostly as a function of peak spawning periods and length of growing season. In Chesapeake Bay, crabs hatched in May may reach 5 to 6 cm (carapace width) in November and 12.7 cm the following August (15 mo to maturity), or crabs hatched in August to September may reach 1.3 cm in November, 7.5 to 10 cm the following November, and 12.7 cm in May (20 mo to maturity) (Van Engel 1958). In southern estuaries of South Carolina, most recruitment to the blue crab pot fishery occurs in September and October for males and October and November for females (Eldridge and Waltz 1977). In Texas and the St. Johns River, Fla., recruitment occurs approximately 1 yr following spawning; therefore peak recruitment in Texas is in May to July and September to October (More 1969), while in the St. Johns River, peak recruitment occurs from March to September (Tagatz 1968a).

Recruitment into the Maryland portion of Chesapeake Bay is determined by reproductive success of blue crabs spawned in the Virginia portion of the Bay and the extent of migrations of juveniles (Sulkin 1977). Year class strength in the Maryland portion of Chesapeake Bay is determined primarily from sampling areas in Tangier and Pocomoke Sounds, which are important nursery areas for early juvenile instars (Dintaman 1982). Abundance of crabs in the size range of 61 to 120 mm carapace width that are sampled in September and October provide a good indication of the following spring's harvest in the Maryland portion of Chesapeake Bay and Maryland's oceanside bays (Dintaman footnote 9).

4.4 Mortality and morbidity

4.42 Factors affecting mortality rates

Factors affecting natural mortality rates of blue crabs include predation, disease, extreme weather conditions, environmental contaminants, and lack of food availability. Presumably, lack of food availability is especially important for blue crab larval stages. Difficulty in quantitating these factors is reflected in the small amount of data present in the literature. Van Engel (1982b) reported that extreme temperature declines during January 1977 and February 1978 in Chesapeake Bay were correlated with high mortalities in Virginia's winter crab-dredge fishery. Also, during winter low pressure centers accompanied by high winds in southern Chesapeake Bay often cause strong onshore surface currents coupled with strong offshore subsurface currents that result in abrasion of blue crabs swept along the bottom in shallow waters (Van Engel 1982b). Gray crab disease was prevalent (percent occurrence not reported) in samples of dead blue crabs during 1966 and 1967 from South Carolina (McKenzie 1970).

4.43 Factors affecting morbidity rates

See section 3.35.

5 EXPLOITATION

5.1 Crabbing equipment

5.11 Gear

In the early years of the Chesapeake Bay fishery, trotlines were the principal gear used for catching hard blue crabs, but eventually the crab pot (patented by Lewis in 1938) became the chief gear for hard blue crabs except during winter (Van Engel 1962). The primary gear in winter in the Virginia fishery is the crab dredge, a heavy, rectangular frame, bearing a 1.8 m (6-ft) toothed drag bar on its lower edge, followed by a mesh bag made of rings, cotton, and twine (Van Engel 1962). Descriptions of commercial crabbing gear include those by Wharton (1954) and Cargo (1954).

Typical Chesapeake Bay crab pots are commonly 0.6 m (2 ft) square, top and bottom, and 53.3 cm (21 in) high, made of 18 gauge steel wire of 2.9 cm mesh (1⅛ in) specially treated with zinc (Warner 1976). Crab pots consist of two to four conical funnels serving as entry ports, a partition separating the "upper" and "lower" section, which utilizes a blue crab's tendency to swim up and away from the bottom if alarmed, and a cylindrical bait "box" in the center of the lower section (Warner 1976). Crab pots are set about 30.5 m (100 ft) apart at the edges of river or bay channels of Chesapeake Bay in depths of 1.8 to 18 m (6 to 60 ft), with actual fishing time averaging 2.5 h/100 pots (Van Engel 1962). The number of pots used by commercial crabbers in Mississippi Sound ranged from 65 to 400 (Perry 1975).

[9] R. C. Dintaman, Tawes State Office Building C-2, 580 Taylor Ave., Annapolis, MD 21401. From "The status of the blue crab population in Maryland's oceanside bays," 21 p. (mimeogr.)

Trotlines are plain cotton twine consisting of bait (eel, other fishes, or chicken parts) tied intermittently to the line 0.4 to 1.6 km (0.25 to 1 mi) set in water depths of 1.5 to 4.5 m (5 to 15 ft). Heavy metal objects, such as engine blocks, are used as anchors at either end, attached to 1.2 to 1.5 m (4 or 5 ft) of chain, a rope pennant, and several plastic (bleach) bottles serving as marker buoys (Warner 1976).

Otter trawls used in North Carolina are generally 10.6 m (33 ft) across the mouth and have 10 cm stretched mesh at the cod end when used primarily to harvest crabs and a 3.1 cm stretched mesh at the end when used primarily to harvest shrimp (Fischler 1965).

Crab dredges and crab scrapes are described briefly in section 5.41.

5.12 Boats

Dredge boats in the Virginia winter dredge fishery are usually 9.7 to 12.2 m (32 to 40 ft) long, with two dredges sometimes towed simultaneously. Boats usually contain a captain plus a crew of two or three persons (Van Engel 1962).

5.2 Blue crab areas

5.21 General geographic distribution

See section 2.1.

5.22 Geographical ranges

See section 2.1.

5.23 Depth ranges

See section 5.1.

5.24 Conditions of the grounds

Pollution by Kepone contamination (Roberts and Leggett 1980) has forced the closure of the blue crab fishery in the James River, Va. Total blue crab catch from the James River estuary declined 90% from 1972 through 1975 (Schimmel et al. 1979), whereas landings from the adjacent Rappahannock River estuary did not decline appreciably over the same period.

5.3 Crabbing seasons

Georgia and Gulf Coast States (Florida, Alabama, Mississippi, Louisiana, and Texas) have no closed season for harvesting blue crabs (Bearden 1978). In South Carolina it is unlawful to trawl specifically for blue crabs in specified offshore areas and sounds from April through November. In Virginia and North Carolina it is unlawful to catch blue crabs with crab scrapes or dredges between 1 April and 1 December and 1 April and 30 November, respectively (Bearden 1978). Capture of hard crabs is unlawful in Maryland waters between 1 January and 1 April. North Carolina and Virginia have designated sanctuary areas in which crabbing is unlawful during certain seasons (Bearden 1978).

5.4 Crabbing operations and results

5.41 Effort and intensity

Catch per unit effort (pounds/pot day = total pounds caught on a given day ÷ number of pots used on a given day) in Mississippi Sound averaged over monthly periods ranged from 1.3 to 7.2 lb (0.6 to 3.3 kg) over a 3-yr period for commercial size crabs (Perry 1975). According to Perry (1975), rises in catch per unit effort accompanied 1) migration periods of mature females into the Sound, 2) fall-winter arrival of females from Lake Borgne, La., and 3) maturation of both sexes in early spring with warming temperatures.

Several studies have evaluated catch efficiencies of various sampling gears, both modified and unmodified, for several size classes of blue crabs. A crab dredge divided equally into lined (1.3 cm mesh) and unlined (7.6 cm mesh) portions had significantly better catch efficiency of crabs $<$ 60 mm carapace width in the lined section (Sulkin and Miller 1975). Also, a lined crab dredge (1.3 cm mesh) had significantly better catch efficiency than a lined oyster dredge (1.2 cm mesh) for two size classes (1-59 and 60-119 mm carapace width). For experimental sampling purposes, no single gear type effectively samples all juvenile stages and adults, all seasons, depths, and bottom types considered (Miller et al. 1980). Comparison of a push net (81.3 cm wide, 60.9 cm high, 0.6 cm stretch mesh bag), a crab scrape (96.5 cm wide, 38.1 cm high, 0.6 cm stretch mesh net), and an otter trawl (working width of 3.6 m, cod end lined with 0.6 cm stretch mesh netting) indicated that the crab scrape had highest catch efficiency (number of crabs/m^2) in each of three carapace width size classes (1 to 20 mm, 20.1 to 40 mm, 40.1 to 60.0 mm). Also, Miller et al. (1980) mentioned that a crab scrape can be operated by one person and is cheaper than an otter trawl.

Sampling studies in the York River, Va. (0 to 15 mi upstream), evaluated the effects of tow duration and attachment or removal of a tickler chain (20 mm link) with a 9.1 m semiballoon trawl on catches of blue crabs (Chittenden and Van Engel 1972). Five-minute tows produced mean catch values similar to either 10- or 15-min tows. Catches almost tripled when the tickler chain was attached to the trawl.

Annual sampling of blue crabs (all sizes) in Maryland from May through October is conducted with a 4.9 m (16 ft) semiballoon otter trawl for 6 min at a speed of 4 kn (Dintaman 1982, footnote 9). Average catch values were lower for 3.6 m (12 ft) and 7.6 m (25 ft) trawls conducted on an experimental basis in the mid-1970's (Dintaman 1982).

5.42 Selectivity

An experimental self-culling crab pot containing two escape rings (6.35 cm diameter) in the top and one (6.35 cm diameter) in the bottom, trapped only 9.5% (72 of 761 crabs caught) sublegal crabs ($<$ 127 mm carapace width) compared with 37.6% sublegal crabs (398 of 1,059) caught in commercial crab pots without escape rings (Eldridge et al. 1979). According to Eldridge et al. (1979), advantages of a self-culling crab pot (3 escape rings, each 6.35 cm diameter) include: 1) Less culling required by law abiding crabbers, 2) less injury to sublegal crabs, and 3) reduced law enforcement problems and fewer deliveries of illegal crabs to processors. Similar studies for ideal escape ring size may be necessary in various regions having a blue crab fishery if length to

width relationships of crabs are appreciably different from those in South Carolina (Eldridge et al. 1979).

5.43 Catches

Commercial blue crab landings (hard crabs) along the Atlantic and gulf coasts of the United States are listed in Tables 7 through 9. Also, commercial fisheries for the peeler and soft crab stage of blue crabs are listed in Table 10. Only Maryland, Virginia, Louisiana, and North Carolina currently have important fisheries for soft shell crabs. Suggested methodology for estimating annual total harvest for blue crabs using simple or stratified random sampling of licensed crabbers via questionnaires was described by Summers, Hoffman, and Richkus (1983) and Summers, Richkus, Hoffman, Bonzek, King, and Burch (1983).

Crab pots and otter trawls are principal gear types for hard crab harvesting in several states. The Georgia blue crab fishery consists mainly of otter trawls and crab traps or pots (Palmer 1974). Over a 5-yr period (1972-76) a mean of 13.4 ± 5.8% of the annual hard crab harvest resulted from shrimp otter trawls and 0.9 to 12.8% of the harvest in different years resulted from crab otter trawls (Wheeland 1975; Pileggi and Thompson 1976, 1978, 1980; Wise and Thompson 1977). Hard crab harvest from pots plus traps averaged 79.9 ± 11.5% over the same 5-yr period. In Alabama, hard crab harvest from 1972 through 1976 averaged 95.9 ± 1.9% from crab pots with the remaining catch resulting from shrimp otter trawl operations (Wheeland 1975; Pileggi and Thompson 1976, 1978, 1980; Wise and Thompson 1977). Likewise, in Mississippi Sound, most of the commercial hard crab catch is harvested with crab pots (Perry 1975). Crab pots produced 95.4 ± 2.3% of the total annual hard crab harvest in Texas from 1972 through 1976. Crab otter trawls in North Carolina contributed 15.6 ± 6.6% of the total hard crab catch from 1972 through 1976, whereas crab pots produced 76.7 ± 7.2% of the hard crab catch. Over a 10-yr period (1965-75), Eldridge and Waltz (1977) estimated that 12% of South Carolina's commercial crab landings were from trawl catches, while most of the remaining catch resulted from crab pots.

The hard crab fishery of Maryland results mainly from crab pots (62.1 ± 3.5%) and trotlines (37.4 ± 3.5%) as indicated by the 1972 to 1976 period (Wheeland 1975; Pileggi and Thompson 1976, 1978, 1980; Wise and Thompson 1977). This represents a larger contribution (total kilograms and percentage of total catch) from trotlines than in any other blue crab fishery. Estimates of blue crabs harvested in 1981 based upon simple and stratified random sampling of licensed crabbers via questionnaires indicated that commercial crab potters and trotliners accounted for 51 and 36% of the annual harvest, respectively (Summers, Richkus, Hoffman, Bonzek, King, and Burch 1983).

Table 7.—Commercial blue crab landings (hard crabs) of New England, Middle Atlantic, and Chesapeake Bay fisheries (in thousands of kg).[1]

Year	Rhode Island	Connecticut	New York	New Jersey	Delaware	Maryland	Virginia
1939	71.5	1.7	18.8	2,174.8	348.7	10,934.4	12,243.0
1940	53.6		29.0	364.3	125.9	6,824.2	10,449.5
1941						5,436.8	7,135.4
1942	37.9	0.1		333.5	177.1	6,377.9	8,464.4
1943			4.8	176.9	10.9		
1944				132.9	10.9	7,788.4	10,863.7
1945							
1946		0.1				11,557.8	12,196.6
1947		1.7		286.0	566.6	11,608.0	15,587.4
1948		1.4	6.7	299.6	662.4	9,361.7	19,382.7
1949		1.5		905.4	1,013.8	10,048.0	18,456.3
1950		0.5	3.8	967.7	2,002.9	12,495.1	21,063.6
1951		0.8	3.2	474.7	2,109.3	12,338.1	17,061.7
1952		1.7	25.8	484.2	567.5	12,484.6	15,225.9
1953	0.4	2.2	34.0	271.5	784.5	11,971.1	14,677.4
1954	13.6	0.9	20.4	395.4	1,322.0	8,659.1	14,741.0
1955		0.9	19.5	286.0	1,276.6	6,915.3	12,206.7
1956		1.8	4.1	314.1	1,706.1	9,628.4	11,688.2
1957		1.4	4.1	551.1	2,234.6	12,879.5	11,295.5
1958		1.4	8.2	394.1	1,114.1	12,301.1	8,060.3
1959		0.9	0.9	446.3	749.1	9,618.9	9,601.2
1960		1.4	0.4	695.9	947.5	12,288.9	17,828.6
1961		1.8	0.4	293.3	344.6	12,102.7	19,965.1
1962		0.9		683.3	855.3	12,558.1	24,366.6
1963		0.4		390.9	236.9	7,688.0	20,946.7
1964		0.4		258.3	142.1	10,233.2	23,413.7
1965		0.4		410.9	247.9	14,527.1	22,955.6
1966				310.5	259.2	13,789.3	28,933.9
1967				210.5	130.8	11,162.9	24,890.1
1968				61.3	101.2	4,242.6	20,357.8
1969				282.4	231.5	10,448.3	15,272.6
1970		0.4		340.9	276.0	11,320.5	19,526.9
1971		0.4		500.8	460.4	11,838.0	21,704.4
1972				652.4	1,158.6	10,660.8	22,043.5
1973				1,167.7	1,077.3	8,870.7	16,682.7
1974				1,246.2	1,020.6	11,195.6	18,545.9
1975				1,302.9	1,612.1	11,015.9	15,807.8
1976				1,223.9	1,618.5	8,821.2	11,695.5

[1] 1939-67 = Fishery Statistics of the United States, U.S. Dep. Inter., Fish Wildl. Serv., Stat. Dig. 1-61. 1968-76 = Fishery Statistics of the United States, U.S. Dep. Commer., NOAA, NMFS, Stat. Dig. 62-70.

Table 8.—Commercial blue crab landings (hard crabs) of South Atlantic fisheries (in thousands of kg).[1]

Year[2]	North Carolina	South Carolina	Georgia	Florida[3]
1939	1,295.7	1,133.5	999.8	2,038.9
1940	1,819.5	1,879.5	1,065.8	2,561.7
1949				[4]933.3
1950	3,032.9	1,302.6	2,282.5	2,799.6
1951	3,551.3	1,156.9	2,963.0	3,956.4
1952	2,797.4	1,182.5	4,294.0	3,692.6
1953	4,761.1	1,709.8	4,206.6	4,303.9
1954	4,416.1	1,129.5	4,830.6	4,462.9
1955	4,303.9	2,108.4	4,878.2	5,737.2
1956	3,743.2	863.5	3,878.1	5,346.7
1957	5,253.7	1,627.1	4,071.5	5,373.0
1958	5,685.4	2,196.9	4,623.0	7,577.3
1959	6,691.5	2,166.5	5,727.6	9,310.6
1960	6,781.0	3,232.9	7,157.8	11,626.9
1961	7,209.5	2,121.1	5,589.6	11,175.6
1962	5,548.3	2,877.0	5,585.6	8,274.1
1963	8,551.1	4,012.0	6,583.0	9,851.3
1964	10,937.8	4,283.9	5,235.5	9,542.0
1965	10,139.6	3,368.7	4,657.6	12,058.7
1966	8,586.9	2,598.7	3,884.4	10,836.9
1967	6,479.5	2,382.1	3,857.1	10,576.4
1968	8,703.2	1,753.3	1,665.7	7,092.8
1969	10,060.2	3,745.5	2,336.7	7,857.8
1970	9,479.5	3,155.3	3,219.8	10,244.5
1971	6,572.1	3,408.6	3,829.5	9,720.6
1972	6,119.5	3,369.6	4,112.8	7,700.3
1973	5,431.2	3,610.2	3,624.7	6,134.9
1974	5,976.5	3,426.8	4,599.5	7,993.1
1975	5,026.7	2,896.5	4,024.7	7,714.4
1976	5,326.3	2,605.9	2,666.3	7,296.7

[1] 1939-67 = Fishery Statistics of the United States, U.S. Dep. Inter., Fish Wildl. Serv., Stat. Dig. 1-61. 1968-76 = Fishery Statistics of the United States, U.S. Dep. Commer., NOAA, NMFS, Stat. Dig. 62-70.

[2] No data for 1941-48.

[3] Includes Atlantic and gulf coast catches, combined.

[4] Gulf coast catch only.

Winter crab dredge fisheries exist in New Jersey, Delaware, and Virginia. Over the 1972 through 1976 period, crab dredging operations contributed an average of 18.6±6.3% of New Jersey's hard crab catch and 21.2±5.1% of Virginia's total annual hard crab catch (Wheeland 1975; Pileggi and Thompson 1976, 1978, 1980; Wise and Thompson 1977). From 1974 through 1976, Delaware's crab dredging operations contributed 15.3±5.1% of that state's hard crab harvest. The large remainder of hard crabs harvested in each of these states was from crab pots or traps (81.3±6.3% for New Jersey and 78.6±5.1% for Virginia).

Since 1960, usage of trotlines in Louisiana for hard crab capture has steadily decreased from 75% of the total catch to 1% in 1977, while hard crabs harvested by crab traps has increased from 1 to 98% over the same period (Roberts and Thompson 1982).

Generally, increases or decreases in catches of hard crabs from one year to the next occur simultaneously for New Jersey and Delaware (Table 6), probably due to dependence on the mouth of the Delaware Bay as a major spawning site for several river populations in both states. Similarly, hard blue crab landings in Virginia and Maryland generally increased or decreased in the same years due to the dependence of crab fisheries in both states on the spawning area at the mouth of Chesapeake Bay (Table 6).

Peeler and soft crabs in Maryland were harvested mainly by crab scrapes (77.8±4.0%), pound nets (10.1±2.2%), and peeler pots (8.2±2.0%) over a 5-yr period from 1972 through 1976. Over the same time interval, 55.1±10% of Virginia's peeler and soft crab harvest resulted from peeler pots, 15.8±8.7% resulted from crab scrapes, and 28.9±11.9% resulted from pound nets.

Table 9.—Commercial blue crab landings (hard crabs) of Gulf Coast States (in thousands of kg).[1]

Year[2]	Alabama	Mississippi	Louisiana	Texas
1939	253.1	667.1	5,097.8	184.5
1940	626.8	675.7	6,384.1	114.6
1948	1,077.1	2,498.2	9,583.8	238.9
1949	966.1	1,890.0	8,114.7	169.8
1950	271.7	1,834.2	5,950.3	175.8
1951	503.5	736.9	3,954.2	127.0
1952	297.5	783.6	3,329.6	153.4
1953	493.5	641.0	3,691.4	196.1
1954	441.3	570.2	3,216.6	172.1
1955	732.3	800.4	4,908.2	161.6
1956	329.2	898.5	4,268.5	88.5
1957	663.7	1,089.6	3,885.8	91.2
1958	536.6	964.3	4,238.5	258.8
1959	496.2	1,363.3	4,344.8	541.2
1960	226.5	1,276.6	4,562.7	1,301.6
1961	380.5	1,137.3	5,407.1	1,305.3
1962	287.8	411.8	4,323.4	2,030.7
1963	588.8	504.8	3,623.8	1,352.9
1964	799.9	583.8	2,584.0	1,127.0
1965	822.6	768.2	4,214.0	1,644.4
1966	991.1	661.5	3,625.0	1,261.2
1967	1,068.3	461.8	3,431.8	1,191.8
1968	898.9	515.7	4,336.2	1,854.1
1969	871.7	789.9	5,267.3	2,879.7
1970	638.8	920.2	4,655.3	2,508.3
1971	906.6	571.6	5,532.4	2,637.7
1972	732.3	618.3	6,847.7	2,934.7
1973	952.5	824.0	10,478.3	3,123.9
1974	829.0	756.8	9,370.6	2,763.9
1975	744.6	516.2	7,783.3	2,720.4
1976	589.8	606.1	6,905.8	3,027.3

[1]1939-67 = Fishery Statistics of the United States, U.S. Dep. Inter., Fish Wildl. Serv., Stat. Dig. 1-61. 1968-76 = Fishery Statistics of the United States, U.S. Dep. Commer., NOAA, NMFS, Stat. Dig. 62-70.

[2]No data for 1941-47.

Since 1957, oceanside blue crabs (hard and soft crabs) have comprised between 1 and 7% of the total annual catch of blue crabs in Maryland on an annual basis (Dintaman footnote 9). During April, the oceanside bays contribute the majority of the total catch of blue crabs in Maryland waters, most of which are intermolt, hard crabs. The primary month for harvest of soft/peeler crabs is usually May in the oceanside bays, followed by peak total blue crab catches (hard, peeler, and soft crabs combined) in Chesapeake Bay from June through September.

Peak harvest months for blue crabs in Alabama (Mobile Bay) are July, August, and September (Tatum 1979). Blue crabs (hard) are harvested primarily from March through October in North Carolina waters, while soft shell crabs are harvested primarily from April through July (Pearson 1951). Peak months for hard crab catches in Louisiana are July and August, whereas lowest monthly yields occur from December through March (Roberts and Thompson 1982). Peak crab pot catches occur from June to November in South Carolina and the trawl fishery for blue crabs operates mainly from December through March (Eldridge and Waltz 1977).

Though recreational fishing for blue crabs is substantial in locations where important commercial fisheries exist, recreational catch statistics for blue crabs are generally not available. Sport crabbers were estimated to land about 22,500 kg (50,000 lb)

Table 10.—Peeler and soft shell blue crab fisheries in the United States (in thousands of kg).[1]

Year	New Jersey	Delaware	Maryland	Virginia	North Carolina	Louisiana
1939	27.8	11.5	1,468.1	1,263.5	78.5	97.5
1940	24.9	9.9	812.9	897.6	129.8	114.3
1941			379.7	776.1		
1942	24.3	4.2	746.9	656.2		
1943	9.9	2.9				
1944	9.6	2.9	504.8	1,099.8		
1945						
1946			1,173.0	745.4		
1947	0.2	1.4	1,366.7	1,109.0		
1948	1.4	4.0	845.5	1,257.8		399.9
1949	5.8	26.2	1,058.3	1,139.4		206.7
1950	6.2	4.3	1,315.7	1,466.6	94.8	164.8
1951	4.6	3.0	412.7	663.1	75.9	159.0
1952	3.6	2.0	720.8	1,002.2	56.4	203.4
1953	2.3	0.9	865.3	1,171.8	76.2	221.6
1954	3.2	1.4	361.8	585.2	43.1	206.6
1955	4.9	3.6	545.2	820.8	11.8	263.8
1956	4.1	0.9	830.4	824.5	32.2	272.4
1957	2.3	0.4	718.7	732.8	29.1	250.2
1958	2.3	0.4	1,482.3	611.9	34.5	261.9
1959	0.4		772.7	689.6	59.3	274.7
1960	7.7	18.2	1,265.8	721.9	41.3	233.4
1961	25.9	24.5	1,222.1	711.9	45.9	281.5
1962	70.8	11.8	1,766.9	611.5	44.5	156.2
1963	15.0	1.4	957.0	430.8	37.7	149.4
1964	4.5	0.9	1,588.1	453.1	31.8	90.8
1965	15.0	5.4	1,223.1	489.9	107.6	92.6
1966	1.8	0.4	855.3	466.7	57.2	58.1
1967	2.3	1.4	992.4	552.5	39.0	66.3
1968	0.4	0.9	454.9	365.9	38.1	128.9
1969	4.1	4.1	1,021.0	894.8	42.2	89.4
1970	15.0	4.5	717.3	413.0	27.2	40.9
1971	5.9	8.2	694.6	314.6	22.2	57.7
1972	6.8	33.1	715.1	389.5	22.7	46.3
1973	10.4	15.4	686.9	446.3	20.4	54.0
1974	57.2	38.6	827.2	369.6	15.0	43.6
1975	17.7		750.9	342.3	9.1	49.9
1976	40.9		669.2	345.4	9.1	40.0

[1]1939-67 = Fishery Statistics of the United States, U.S. Dep. Inter., Fish Wildl. Serv., Stat. Dig. 1-61. 1968-76 = Fishery Statistics of the United States, U.S. Dep Commer., NOAA, NMFS, Stat. Dig. 62-70.

annually in Mississippi waters (Herring and Christmas 1974, cited in Perry 1975). Tatum (1979) estimated that the recreational catch equals about 20% of the commercial catch in Mobile Bay, Ala.

6 PROTECTION AND MANAGEMENT

6.1 Regulatory measures

6.11 Limitation or reduction of total catch

Minimum sizes allowed for harvest of hard crabs, peelers, and soft crabs in various states are listed in Table 11. Since the minimum harvestable size for hard crabs is 10.2 cm (4 in) in Alabama, percentage of immature females compared with mature females harvested should be evaluated to determine if the minimum size is permitting capture of too many immature females.

Table 11.—Minimum size limits and laws regarding protection of females for various states having blue crab fisheries.[1]

State	Minimum size limits	Laws protecting females
Delaware[2]	Hard crabs—5 in	Possession of egg bearing females caught in Delaware waters unlawful
Maryland	Hard crabs—5 in[3] Peelers—3 in Soft crabs—3.5 in	Possession of egg bearing females caught in Maryland waters unlawful
Virginia	Hard crabs—5 in (Adult females, peelers and soft crabs exempt)	Unlawful to catch female crabs within a designated sanctuary area from 15 May to 15 September
North Carolina	Hard crabs—5 in (Peelers exempt)	None
South Carolina	Hard crabs—5 in (Crabs in commercial shedding floats exempt)	Possession of egg bearing females caught in South Carolina waters unlawful
Georgia	Hard crabs—5 in Peelers—3 in Soft crabs—3 in	Unlawful to retain spawning females May or June
Florida	Hard crabs—5 in	Unlawful to sell egg bearing blue crabs
Mississippi	None	Unlawful to harvest sponge crabs from south of intracoastal waterway, commencing at Alabama-Mississippi boundary and running west to Gulfport-Ship Island Channel
Alabama	Hard crabs—4 in	None
Louisiana	Hard crabs—5 in Soft crabs—4.5 in	Retention of berried females unlawful

[1]From Bearden (1978).
[2]From Miller (1976).
[3]Mature females may be harvested in Maryland regardless of size.

6.12 Protection of portions of population

Laws protecting gravid (i.e., berried, sponge, egg bearing) females in various states are listed in Table 11. Eldridge and Waltz (1977) reported that 85% of immature females captured in commercial crab pots were less than the minimum legal size of 5 in (127 mm) carapace width in several South Carolina estuaries. Therefore, the authors suggested that retention of immature females, regardless of actual size, should be discouraged.

6.4 Control or alteration of the biological features of the environment.

6.41 Control of aquatic vegetation

The importance of eelgrass as a habitat for blue crabs has prompted investigations to evaluate the causes for its decline in abundance in Chesapeake Bay as well as methods of restoration of eelgrass beds and evaluation of limiting factors for growth of eelgrass. Orth (1977) induced significant increases in biomass of eelgrass in fertilized (5 or 10% NH_4NO_3, 10% P_2O_5, 10% K_2O) plots compared with unfertilized, adjacent plots in Chesapeake Bay off Church Neck on the "Delmarva" Peninsula, Va.

6.5 Artificial stocking

An attempt to supplement a natural population of blue crabs near Crisfield, Md., by means of ovigerous females in shedding floats, failed because of low survival of the females, possibly as a result of transport from the areas of capture (Graham and Beaven 1942). Additionally, larval survival rate was low since salinity was probably below the minimum level of 18‰ for successful hatching (Davis 1965) and below the minimum level of 20‰ for early larval development (Costlow and Bookhout 1959). Dramatic increases occur in survival rate of blue crabs in the laboratory beginning with the first crab stage (Millikin 1978; Millikin et al. 1980) compared with larval stages reared in the laboratory (see section 3.22). This suggests that any attempts to supplement natural populations would more likely be successful if early juvenile stages were used.

7 SOFT CRAB SHEDDING OPERATIONS

7.1 Use of cultured blue crabs

Blue crabs are often harvested in the peeler stage (1 to 3 d premolt) in Maryland, Virginia, North Carolina, and Louisiana for subsequent culture until ecdysis in shedding floats in natural waters or land-based flow-through shedding tanks located near natural waters. Blue crabs still in the soft shell stage (A_1), especially < 3 to 6 h after molting, are removed from water to prevent further shell hardening (exocuticle mineralization) and packed in ice for shipment or stored frozen for eventual human consumption. Also, peeler crabs of a minimum size of 3 in (7.6 cm) are often sold as bait for sport fishing in Chesapeake Bay (Haefner and Garten 1974).

7.2 Procurement and maintenance of stock

Blue crabs are harvested in the peeler stage by several gear types, mainly as a function of mating season and location of vegetated areas which can provide refuge for crabs from predators during the soft shell stage. Peeler pots are larger versions of commercial crab pots but with smaller mesh (2.5 cm). Usually, peeler pots are "baited" with two or three live, adult male crabs which may attract as many as 20 or 30 female peelers approaching their terminal molt into the peeler pots (Warner 1976). Use of bare pots (without bait or large male crabs) is less common and used in areas devoid of bottom vegetation, where the pot may appear to be a refuge to peeler stage crabs. Peeler pounds consist of a wire lead (2.5 cm mesh) oriented perpendicular to the shore which channels peelers into the head section which is 0.08 × 0.11 × 0.14 m (3 × 4 × 5 ft) which is not completely covered at high tide (Otwell and Cato 1982). Crab scrapers in Chesapeake Bay harvest the largest portion of peelers and soft crabs, catching as many as 200 to 500/d during peak occurrence of mating, mostly in seagrass beds (Warner 1976). The first peak occurrence of peelers in Chesapeake Bay occurs in the third or fourth week of May (water temperature approaching 18°C) near a full moon (Warner 1976). Experimental work in South Carolina, designed to determine the best methods for

harvesting peelers in that area, indicated a peak run of female peelers preparing for their terminal molt during the waxing and waning of the full moon in April (Bishop et al. 1982, 1983). Optimal methods for peeler crab capture in South Carolina were evaluated by comparing hard crab pots, fyke nets, bush lines, habitat pots (similar to hard crab pots except with 2.5 cm mesh, covered with interwoven plastic flagging tape and unbaited), and peeler pots (Bishop et al. 1983). Crab scrapes were not evaluated due to the lack of subtidal grass beds in South Carolina. Bush lines and fyke nets were unsuccessful because of the strong tidal currents ($>$ 1.8 km/h) and large tidal amplitude (1.5 m = mean) in South Carolina. Large intertidal areas of marsh may also have rendered bush lines less effective. Habitat pots captured 2.5 times as many male peelers as female peelers and 2.5 times as many late premolt crabs (6 d or less premolt) as early premolt crabs (7 to 14 d premolt). Hard crab pots captured the highest amount of peelers/gear-day, but culling and damage to peelers from intermolt crabs reduces this gear's effectiveness. Peeler pots only captured good numbers of peelers during the full moon of April. Bush lines are unique to the Louisiana soft crab fishery and consist of six or seven branches of wax myrtle, *Myrica cerifera*, bound together at the bases and tied to the crabbing line at regular intervals (Jaworski 1972).

Soft shell crab production has historically been low in South Carolina, Georgia, Florida, Alabama, Mississippi, and Texas. According to Perry et al. (1982), minimal growth of the soft crab industry in these states is primarily the result of lack of a reliable source of supply of peeler crabs.

Initial investigations have suggested that heated effluents in discharge canals from power plants may provide a feasible culture medium for soft shell crab production during winter (Reimer and Strawn 1973; Parker et al. 1976). The main season for soft shell crab production is April to October in Chesapeake Bay and March to October in Louisiana (Reimer and Strawn 1973).

7.4 Spawning

See sections 3.17, 3.21, and 3.22.

7.5 Shedding operation management

Molting signs on the translucent penultimate and ultimate segments of the fifth pair of pereopods (swimming paddles) of juvenile and adult blue crabs include the following: 1) White sign or line (7 to 14 d), 2) pink sign or line (3 to 6 d), and, 3) red sign or line (1 to 3 d premolt) (Van Engel 1958; Warner 1976; Perry et al. 1982). External signs often associated with the red sign stage are possession of well developed, limb buds due to regeneration of autotomized pereopods or changes in the color of the abdomen of an immature female approaching her pubertal molt from creamy white to reddish purple (Perry et al. 1982). Other external characters related to molt stage that are commonly used within commercial shedding operations or by crabbers are: 1) Papershell (slightly stiff exoskeleton, 12 h postmolt), 2) buckram (crinkly hard exoskeleton, 24 h postmolt), and 3) external carapace similar to intermolt (72 h postmolt) (Warner 1976).

At least four or five shedding floats or tanks are desirable to separate various molt stages, such as white line, pink line, red line, and busters (crabs that are molting) (Van Engel 1958) into different containers (Bearden et al. 1979). Pine wood shedding floats constructed with laths on the sides and ends for water circulation are often about 3.7 m long $\times$ 1.1 m wide $\times$ 0.3 m to 0.45 m deep with 23 cm of water depth in the float (Beaven and Truitt 1940).

Nicking, a process whereby crabbers push in the free or movable segment (dactyl) of the cheliped until it snaps and becomes nonfunctional, is often performed to reduce cannibalistic behavior in shedding operations. However, excessive bleeding or swelling may result in lowered rates of successful molting (Beaven and Truitt 1940; Haefner and Garten 1974) or potentially harmful bacterial infection (Johnson[10]).

Although blue crabs occur in a wide range of salinities (see section 1.36), recently harvested peelers should not be placed in shedding tanks having a salinity more than 10‰ different from the area of harvest (Haefner and Garten 1974).

Eyestalk removal from the megalopal stage of blue crabs in the laboratory promotes molting (Costlow 1963b), since the molt-inhibiting hormone occurs in the X-organ/sinus gland complex within the eyestalks. Still, removal of eyestalks of blue crabs of peeler size or larger is not recommended because of high mortality rates of subadults and adults following this procedure (Van Engel 1982a).

7.6 Foods; feeding

Blue crabs in the peeler stage or buster stage do not require food, since feeding activity temporarily ceases until after molting (Van Engel 1958; Haefner and Garten 1974; Johnson 1980). Observed final feeding activity prior to ecdysis occurred at variable time intervals for 79 molts undertaken by 68 crabs (2.9 to 6.9 cm carapace width) reared in the laboratory (Millikin unpubl. data) as follows:

Last day of feeding activity prior to molting (d)	*Frequency (number of molts)*
7	3
6	9
5	6
4	7
3	14
2	26
1	14

It is noteworthy that these crabs were acclimated to laboratory culture conditions, whereas recently harvested peelers that are placed in shedding tanks do not have time to acclimate before ecdysis. Nevertheless, these data strongly suggest that blue crabs in natural waters derive nutritional benefit from feed consumption up to and including part of the "red sign stage." Therefore, laboratory-acclimated crabs should be offered food at least through the white sign and pink sign stages prior to molting.

7.7 Diseases

See section 3.35. Shell disease and paramoebiasis are two diseases that sometimes occur in shedding operations (Sindermann 1977a; Johnson 1977f). Also, if early premolt crabs that are still feeding are mistakenly placed in shedding tanks with late premolt peeler stage crabs, bacterial infection in late premolt peelers may result from wounds inflicted by the early premolt crabs.

[10]P. T. Johnson, Northeast Fisheries Center Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654, pers. commun. July 1982.

ACKNOWLEDGMENTS

We thank Phyllis T. Johnson for contributing Table 2 and portions of "Viral infections" and "Bacterial infections" in section 3.35. This manuscript benefitted from critical reviews by L. Eugene Cronin, Phyllis T. Johnson, Charles Biernbaum, Peter J. Eldridge, James M. Bishop, Patricia H. Fair, Alan R. Fortner, and Lowell V. Sick. Sections of the manuscript were also reviewed by Bruce Collette, John D. Costlow, and C. G. Bookhout. We are grateful to John Costlow and C. G. Bookhout for permission to use their figures on blue crab larval stages of development which were previously published in the *Biological Bulletin*. We thank Sandra West for typing several drafts of the manuscript. M. Millikin is especially grateful to Charles Wenner for his encouragement during preparation of earlier drafts of this synopsis.

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